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FÁBIO VITALINO SANTOS ALVES

ESTUDOS MACROEVOLUTIVOS NA SUBTRIBO LYCHNOPHORINAE (ASTERACEAE: VERNONIEAE): DIVERSIFICAÇÃO, BIOGEOGRAFIA E EVOLUÇÃO DE NICHO

Recife – PE
2022

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de mestre em Biologia Vegetal.

Área de concentração: Sistemática e Evolução (Taxonomia e Filogenia Molecular)

Orientador: Prof. Dr. Benoît Francis Patrice Loeuille

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RESUMO

A subtribo Lychnophorinae está presente no domínio Cerrado, com a maior parte das espécies distribuídas nos campos rupestres da Cadeia do Espinhaço, tipo vegetacional marcante que ocorre em afloramentos rochosos de áreas montanhosas. Pouco se sabe sobre o processo macroevolutivo do grupo e possíveis variáveis que influenciaram a sua distribuição atual. Além disso, as espécies do Cerrado são reconhecidas por estarem sob constante ameaça ambiental devido a pressões decorrentes de mudanças climáticas e atividades antrópicas, entretanto, o conhecimento sobre conservação das espécies da subtribo é escasso. Não obstante, variações climáticas e processos regulares de incêndios ao longo da evolução podem ter influenciado o processo de diversificação e história biogeográfica do grupo. Os objetivos deste estudo foram: 1) identificar os tempos de divergência existentes através de construção e datação da árvore filogenética; 2) descobrir o alcance das áreas ancestrais e os processos biogeográficos existentes ao longo da evolução; 3) determinar os estados de caracteres ancestrais e como os principais caracteres podem ter influenciado a diversificação; 4) descobrir possível influência dos regimes de incêndios do Cerrado para a distribuição e evolução das espécies; 5) detectar a influência das oscilações climáticas na distribuição das espécies do gênero *Eremanthus* dentro da perspectiva evolutiva e de conservação; 6) caracterizar o status de ameaça para espécies de *Eremanthus*. Para isso, a árvore filogenética de Lychnophorinae foi reconstruída através de máxima verossimilhança e datada através de penalized likelihood. Foram realizadas reconstruções de estados de caracteres ancestrais para os principais caracteres morfológicos e reconstrução da área ancestral através da construção de modelos biogeográficos. Foram realizadas modelagens de nicho das espécies do gênero *Eremanthus* para identificação de áreas de adequabilidade em diferentes períodos de tempo. As espécies de *Eremanthus* foram submetidas a avaliação de risco de extinção através dos critérios adotados pela IUCN. Desta forma, estima-se que a subtribo tenha surgido durante o Mioceno, com maior número de características morfológicas importantes surgindo durante o Pleistoceno (e.g., pappus setoso e bainha pad-like), além de apresentar importantes eventos de dispersão fundadora ao longo da história biogeográfica. Os modelos climáticos das espécies de *Eremanthus* corroboram com a Hipótese de Refúgio do Pleistoceno e a avaliação do status de conservação das espécies revelou possíveis riscos de extinção futura decorrentes de mudanças climáticas e ações antrópicas.

Palavras-chave: biogeografia; campos rupestres; cerrado; conservação; evolução; modelagem.

ABSTRACT

The Lychnophorinae subtribe is present in the Cerrado domain, with most species distributed in the rocky fields of the Espinhaço Range, a striking vegetation type that occurs in rocky outcrops of mountainous areas. Little is known about the group's macroevolutionary process and possible variables that influenced its current distribution. In addition, Cerrado species are recognized for being under constant environmental threat due to pressures arising from climate change and human activities, however, knowledge about conservation of species in the subtribe is scarce. Nevertheless, climatic variations and regular fire processes throughout evolution may have influenced the group's diversification process and biogeographic history. The objectives of this study were: 1) to identify the existing divergence times through the reconstruction and dating of the phylogenetic tree; 2) discover the reach of ancestral areas and biogeographic processes existing throughout evolution; 3) determine the ancestral character states and how the main characters may have influenced the diversification; 4) discover the possible influence of fire regimes in the Cerrado on the distribution and evolution of species; 5) detect the influence of climatic fluctuations on the distribution of *Eremanthus* species from an evolutionary and conservation perspective; 6) characterize the threat status for *Eremanthus* species. For this, the phylogenetic tree of Lychnophorinae was reconstructed using maximum likelihood and dated using penalized likelihood. Reconstructions of ancestral character states for the main morphological characters and reconstruction of the ancestral range through the construction of biogeographic models were carried out. Niche modelling of species of the *Eremanthus* genus was carried out to identify areas of suitability in different periods of time. The species of *Eremanthus* were submitted to an extinction risk assessment using the criteria adopted by the IUCN. Thus, it is estimated that the subtribe emerged during the Miocene, with a greater number of important morphological characteristics appearing during the Pleistocene (e.g., pappus setose and pad-like sheath), in addition to presenting important founding dispersal events throughout biogeographic history. The climate models of *Eremanthus* species corroborate the Pleistocene Refuge Hypothesis and the assessment of the conservation status of the species revealed possible risks of future extinction arising from climate change and anthropogenic actions.

Keywords: biogeography; campos rupestres; cerrado; conservation; evolution; modelling.

SUMÁRIO

1 INTRODUÇÃO

1.1 ASTERACEAE E LYCHNOPHORINAE

A diversificação de Asteraceae ocorreu de forma intensa no Eoceno impulsionada por mudanças climáticas que ocorreram desde o fim do Cretáceo, favorecendo importantes eventos de dispersão, e atualmente é composta por aproximadamente 25.000–30.000 espécies e responsável por cerca de 10% da diversidade de Angiospermas, sendo a maior e mais diversa família dentre Angiospermas (KEELEY; CANTLEY; GALLAHER, 2021; MANDEL et al., 2019). A família possui uma grande representatividade em áreas abertas e montanhosas, apresentando uma taxa de riqueza de espécies elevada em vegetação de campos rupestres (considerada a família com maior número de espécies neste ambiente) e o maior nível de endemismo circunscrito nesse tipo vegetacional (CAMPOS et al., 2019; FLORA DO BRASIL 2020).

A subtribo Lychnophorinae (Asteraceae: Vernonieae) é composta por 128 espécies distribuídas em 19 gêneros, com ocorrência principalmente em campos rupestres e distribuição quase restrita ao domínio do Cerrado, contendo representantes bem estabelecidos e dominantes nestas áreas (LOEUILLE et al., 2015; LOEUILLE; SEMIR; PIRANI, 2019). A maior parte das espécies são arbustos e arvoretas com indumento composto por tricomas com 3–5 braços, bainha foliar, sincefalia (i.e., capítulos secundários), apêndices apicais das anteras com paredes celulares espessas, ausência de nó basal no estilete, pólen sublofado e pápus paleáceo (decíduo a caduco) (LOEUILLE; SEMIR; PIRANI, 2019).

1.2 DIVERSIDADE NO CERRADO E CAMPOS RUPESTRES

O Cerrado compreende uma área de cerca de 2.000.000 km^2 no Planalto Central do Brasil, sendo a maior savana Neotropical, composta por uma grande riqueza de espécies endêmicas e variabilidade de composição fitofisiográfica (campo limpo, campo sujo, campo cerrado, cerrado sensu stricto, cerradão) e faz fronteira com os tipos vegetacionais da Caatinga, Chaco, Floresta Amazônica, Floresta Atlântica e Pantanal (VIEIRA et al., 2019). Este domínio biogeográfico possui um regime de incêndios bastante marcante que influencia a sua composição florística através da interferência na fenologia e condições adaptativas das plantas (RISSI et al., 2017; SIMON; PENNINGTON, 2012).

Os campos rupestres são compostos por um mosaico vegetacional em afloramentos rochosos montanhosos presentes em altitudes superiores a 900 m e com elevado índice de riqueza de espécies e endemismo (FERNANDES et al., 2020; GIULIETTI; PIRANI; HARLEY, 1997; SILVEIRA et al., 2016). São compostos predominantemente por vegetações herbáceas e arbustivas associadas a solos oligotróficos litólicos, arenosos e rasos, com déficit marcante em fósforo (P) e nitrogênio (N), reflexo da pedogênese, onde a vegetação, constantemente sobre influência de oscilações diárias de temperatura, exposição ao vento e restrições hídricas sazonais, adota estratégias diferenciadas para aquisição dos nutrientes disponíveis em gradientes (ABRAHÃO et al., 2019; BRUM et al., 2017; OLIVEIRA et al., 2016; RAPINI et al., 2008; SILVA et al., 2015).

1.3 CAPÍTULOS DA DISSERTAÇÃO

A dissertação teve como principais propósitos: 1) realizar a construção e datação da árvore filogenética de Lychnophorinae; 2) reconstruir os estados ancestrais dos principais caracteres morfológicos que podem ter influenciado a diversificação das Lychnophorinae; 3) reconstruir a história biogeográfica da subtribo; 4) estimar tempo de divergência do grupo; 5) investigar a influência do regime de incêndios em campos rupestres e cerrado; 6) identificar os potenciais fatores que influenciaram a distribuição do gênero *Eremanthus* através da modelagem de nicho; 7) avaliar o status de risco de extinção das espécies de *Eremanthus*.

A pesquisa foi subdividida em duas partes, descritas em dois capítulos distintos e organizados na estrutura de manuscrito. Detalhes sobre as normas dos periódicos encontram-se nos anexos. Foi realizado um levantamento bibliográfico inicial a fim de aprofundar os temas e métodos aplicados à dissertação, especialmente no que tange à estudos filogenéticos realizados com inclusão de datação, histórico de Lychnophorinae e possíveis questionamentos científicos a respeito do grupo. De igual importância foi a pesquisa e elaboração do banco de dados necessários para as análises subsequentes.

O primeiro capítulo teve por objetivo investigar os principais caracteres morfológicos, diversificação de espécies e história biogeográfica através da reconstrução da árvore filogenética de Lychnophorinae e trata da execução dos estudos e análises filogenéticas, com o desenvolvimento da árvore datada, reconstrução dos estados de caracteres ancestrais em cada nó da filogenia, identificação do número de linhagens que surgiram ao longo do tempo, cálculo do sinal filogenético das principais características morfológicas e identificação das áreas ancestrais na árvore filogenética.

O capítulo seguinte possui o foco apenas no gênero *Eremanthus*, pois é o segundo maior gênero da subtribo e sua distribuição geográfica engloba quase toda a distribuição de Lychnophorinae, além de não haver tempo hábil para executar as análises para todas as espécies da subtribo devido ao tamanho do grupo. Este capítulo buscou investigar os possíveis fatores atuantes na composição da distribuição de *Eremanthus* através do estudo de nicho, considerando também o regime de incêndios em campos rupestres, e os riscos ambientais e de extinção de espécies. Deste modo, foram elaboradas modelagens de nicho em diferentes períodos de tempo para entender as possíveis causas da atual distribuição de suas espécies, a influência de processos históricos na dinâmica do grupo e qual será o futuro das espécies frente as alterações de adequabilidade ambiental provocadas por mudanças climáticas e influência antropogênica. Além disso, é apresentado uma proposta de classificação de risco de extinção das espécies trabalhadas na modelagem e um gap analysis mostrando o percentual de registros e nicho das espécies de *Eremanthus* em áreas de proteção ambiental.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 A SUBTRIBO LYCHNOPHORINAE

De acordo com Loeuille, Semir, Pirani (2019), a definição histórica da subtribo Lychnophorinae (Asteraceae: Vernonieae) corresponde ao agrupamento por Bentham (1873) das espécies de Vernonieae que apresentam capítulos com número reduzido de flores (às vezes até uma única flor) frequentemente organizados em um sincéfalo (i.e., capítulo secundário) e com pappus paleáceo. Porém, Robinson et al. (1980) e Robinson (1992, 1999) modificaram posteriormente a circunscrição do grupo, excluindo ervas com sincéfalo (e.g., *Chresta*) e incluindo gêneros com capítulos não agrupados em sincéfalos (e.g., *Piptolepis*). De forma mais recente, o grupo sofreu uma ampliação importante de seu conceito através da inclusão dos gêneros *Albertinia*, *Blanchetia* e *Gorceixia* e das subtribos Centratherinae e Sipolisiinae, decorrente dos estudos filogenéticos realizados por Loeuille et al. (2015) e Loeuille, Keeley, Pirani (2015), utilizando dados morfológicos e moleculares (ETS, ITS, *ndh*F, *rpl*32-*trn*L, *trn*L-F). Atualmente o grupo contém 131 espécies com espécies descritas recentemente nos gêneros *Eremanthus*, *Lychnocephalus*, *Lychnophora*, *Lychnophorella* e *Piptolepis*. (BONFIM E CÂNDIDO; LOEUILLE, 2020; CÂNDIDO; LOEUILLE, 2021; GOMES; LOEUILLE, 2021; LOEUILLE et al., 2022; MARQUES et al., 2021), demonstrando a necessidade de maiores esforços taxonômicos para descrever a diversidade das Lychnophorinae.

As espécies da subtribo apresentam hábitos desde ervas de poucos centímetros até árvores que alcançam 7 m, caules com presença de fitomelaninas, folhas com grande diversidade de formatos e texturas, possuindo filotaxia alterna, bainha foliar e venação geralmente camptódroma, indumento tomentoso a densamente lanato, tornando-se parcial ou totalmente glabro com o envelhecimento da planta, composto frequentemente por tricomas com 3-5 braços que têm um papel na absorção da água da neblina (BOANARES et al., 2019; ELLER; LIMA; OLIVEIRA, 2016; LOEUILLE et al., 2015; LOEUILLE; KEELEY; PIRANI, 2015; LOEUILLE; SEMIR; PIRANI, 2019; LUSA; LOEUILLE; APPEZZATO-DA-GLÓRIA, 2018). Lychnophorinae ainda apresenta importantes características morfológicas como o sincéfalo (podendo ser de segunda ordem (e.g., *Eremanthus*) ou terceira ordem (e.g., *Lychnocephalus*)), pappus paleáceo decíduo a caduco, anteras calcaradas com parede celular espessa e aglandulares, ausência de nó basal no estilete e pólen tricolporado, equinado e sublofado (LOEUILLE; SEMIR; PIRANI, 2019). Além disso, o grupo possui lactonas sesquiterpênicas, derivados do ácido trans-cinâmico, poliacetilenos e flavonóides como importantes metabólitos secundários, sendo a principal sinapormofia de Lychnophorinae a presença de heliangolídeos (uma classe de lactona sesquiterpênica) nas porções aéreas das espécies que atuam como um dos mecanismos de defesa contra herbivoria, bastante comuns em Asteraceae e especialmente diversificadas na subtribo (LOEUILLE et al., 2015; LOEUILLE; KEELEY; PIRANI, 2015; LOEUILLE; SEMIR; PIRANI, 2019).

Exceto por *Centratherum punctatum* que apresenta ampla distribuição na faixa tropical em diversos continentes e algumas poucas espécies alcançando áreas elevadas da Bolívia, as espécies da subtribo são endêmicas do Brasil, ocorrendo no domínio Cerrado, com destaque para a Cadeia do Espinhaço (ALVES; LOEUILLE, 2021; LOEUILLE; SEMIR; PIRANI, 2019). É nessa formação montanhosa que se encontra o maior índice de riqueza de espécies do grupo (especialmente no Espinhaço Meridional), apresentando diversos padrões de distribuição importantes (alguns exclusivos do grupo), estando presente em áreas de campos rupestres quartzíticas e também em vegetação de canga no Quadrilátero Ferrífero (ALVES; LOEUILLE, 2021; LOEUILLE et al., 2015; LOEUILLE; KEELEY; PIRANI, 2015; LOEUILLE; SEMIR; PIRANI, 2019).

2.2 CADEIA DO ESPINHAÇO: OROGENIA E AMBIENTE

A orogenia da Cadeia do Espinhaço, segunda maior cadeia montanhosa da América do Sul, proporcionou a heterogeneidade ambiental existente entre as montanhas e depressões presentes ao longo dessa formação geológica, contribuindo significativamente para o direcionamento adaptativo das espécies de Angiospermas na região através do isolamento de fragmentos de habitat (ALVES; LOEUILLE, 2021; BITENCOURT; RAPINI, 2013; CONCEIÇÃO et al., 2016). Essa cadeia de montanhas se estende da bacia hidrográfica baiana do rio São Francisco até a Serra do Ouro Branco, entre os estados da Bahia e Minas Gerais, respectivamente, com aproximadamente 1.100 km de comprimento, largura entre 50 e 100 km e blocos constituintes possuindo origem geológica datada do Pré-Cambriano (FERNANDES et al., 2018; GIULIETTI; PIRANI, 1988).

Pertencente geologicamente ao Supergrupo Espinhaço que se desenvolveu por volta de 1,7 Ga e onde atualmente é reconhecido o cráton do São Francisco, a Cadeia do Espinhaço é composta por duas formações principais separadas pelo Corredor do Paramirim (uma zona de deformação envelhecida brasiliana): a Chapada Diamantina, área elevada presente na região centro-norte da Bahia, e a Serra do Espinhaço, formação que se estende desde o sul da Bahia até Minas Gerais, com este último bloco subdividido em Espinhaço Setentrional, cadeia de montanhas formadas por rochas metassedimentares e metavulcânicas que se estende do sul da Bahia até o norte de Minas Gerais, e Espinhaço Meridional, constituído por montanhas presentes na região centro-sul de Minas Gerais (DANDERFER et al., 2009; DANDERFER;

DARDENNE, 2002; DUSSIN; DUSSIN, 1995; PEDROSA-SOARES; ALKMIM, 2013; SAADI, 1995).

Granitos arqueanos, gnaisses, migmatitos e xisto máfico estão entre as rochas mais antigas do Espinhaço Meridional, e sobre elas há uma unidade metavulcanossedimentar composta principalmente por xistos e quartzitos (KUCHENBECKER; SANGLARD, 2018). Esse segmento da Cadeia do Espinhaço é decorrente do cinturão de dobras Araçuaí (um cinturão metamórfico) com origem no Neoproterozóico (~900 Ma), sendo identificado como a principal área de endemismo e centro de origem de diversas espécies endêmicas dos campos rupestres, possivelmente devido a estabilidade ambiental de áreas elevadas que serviram de fonte de diversidade genética para a expansão de linhagens durante o período glacial, sendo, portanto, caracterizada como uma área OCBIL (paisagens muito antigas, climaticamente protegidas e inférteis) (CHEMALE et al., 2012; DUSSIN; DUSSIN, 1995; ECHTERNACHT et al., 2011; INGLIS; CAVALCANTI, 2018).

O Quadrilátero Ferrífero está presente no limite sul do Cráton do São Francisco e se estende por uma área de aproximadamente 7200 km^2, apresentando formações montanhosas com altitudes que variam de 1000 a 2000 m compostas por camadas superficiais de ferro no solo (SAMPAIO et al., 2018; SKIRYCZ et al., 2014). Embora os geologistas não considerem essa formação como parte da Cadeia do Espinhaço por estar presente no Supergrupo Minas, biólogos a consideram parte integrante das montanhas do Espinhaço devido as similaridades biológicas compartilhadas (ECHTERNACHT et al., 2011). O Quadrilátero Ferrífero é composto por quatro unidades litoestratigráficas Arqueana-Paleoproterozóicas definidas por rochas metavulcânicas e metassedimentares de baixo a médio grau do Supergrupo Arqueano Rio das Velhas; Grupo Itacolomi composto por arenito paleoproterozóico e conglomerado; rochas metassedimentares de baixo a médio grau do Neoarqueano-Paleoproterozóico que constituem o Supergrupo Minas e os gnaisses, migmatitos e granitóides que formam os complexos metamórficos do Arqueano (FARINA et al., 2016; SAMPAIO et al., 2018). Apresenta complexos compostos por granitóides e gnaisses do Arqueano circundados por cinturões de rochas supracrustais com origem no Paleoproterozóico, apresentando formações de canga que ocupam uma área de aproximadamente 100 km^2 dispersa em formações montanhosas com altitudes entre 600 e 700 m (FARINA et al., 2016; SKIRYCZ et al., 2014).

O clima da Cadeia do Espinhaço é mesotérmico-Cwb (classificação de Köppen) apresentando invernos secos (entre junho e setembro) e verões chuvosos (principalmente entre novembro e fevereiro), definida pela sazonalidade do clima subtropical, com temperatura média anual de 20.7 ºC e índice pluviométrico médio anual de 1321.07 mm (ALVARES et al., 2013;

CRUZ et al., 2014; ECHTERNACHT et al., 2011). A principal fitofisionomia da Cadeia do Espinhaço são os campos rupestres, presentes em altitudes a partir dos 900 m. Esse tipo vegetacional é composto por um mosaico de afloramentos rochosos envolto em um ambiente fragmentado com solo caracteristicamente raso, arenoso, ácido e pobre em nutrientes, o que favorece o alto índice de endemismo da região (COLLI-SILVA; VASCONCELOS; PIRANI, 2019; FERNANDES et al., 2018; GIULIETTI; PIRANI, 1988). Ocupando menos de 1% do território brasileiro e apresentando elevados índices de diversidade, abrigando cerca de 17% da biodiversidade botânica do país, os campos rupestres sofrem constantemente com as alterações ambientais antrópicas devido a agropecuária e mineração agressivas (FERNANDES et al., 2018).

2.3 O DOMÍNIO CERRADO

O Cerrado é a maior savana Neotropical com aproximadamente 2 milhões de km^2 e está presente na região central do continente sul americano, conectando o Chaco ao sudoeste e a Caatinga ao nordeste e formando um corredor diagonal de habitats secos, estabelecendo uma barreira biogeográfica entre a Amazônia ao noroeste e Mata Atlântica ao sudeste (COLLI; VIEIRA; DIANESE, 2020; SIMON; PENNINGTON, 2012). Três das maiores bacias hidrográficas da América do Sul estão abrigadas nesta fitofisionomia (Bacias Amazônica, do Rio da Prata e do Rio São Francisco), representando cerca de 43% das águas superficiais disponíveis fora da Amazônia, além de ser um hotspot de biodiversidade global abrigando mais de 4800 espécies endêmicas de plantas e vertebrados (DUTRA E SILVA, 2020; STRASSBURG et al., 2017).

A produção de biomassa de gramíneas, a fenologia da vegetação, a respiração do solo e as taxas de assimilação de carbono são as principais variáveis responsáveis pelos processos do ecossistema que sustentam à umidade do solo (LENZA; KLINK, 2006; MIRANDA et al., 1997; SANTOS et al., 2003). O Cerrado é responsável por uma ampla rede aquífera que abastece importantes bacias hidrográficas e a localização desta fitofisionomia agregada a sua elevada altitude e solos profundos são fundamentais para a proteção e sustentação dos recursos hídricos (KLINK et al., 2020). Além disso, a região é importante para a manutenção da qualidade da água decorrente da conservação da mata ciliar ao longo dos rios (CORDEIRO et al., 2020; HUNKE et al., 2015; LIMA et al., 2011; VALERA et al., 2019).

Embora a composição biótica atual tenha seu estabelecimento recente, as espécies do Cerrado possivelmente são oriundas evolutivamente de um ecossistema pré-savana com origem estimada no período Cretáceo (AGUIAR et al., 2020; RATTER; RIBEIRO; BRIDGEWATER, 1997; SIMON et al., 2009). A formação do Cerrado é atribuída principalmente às mudanças climáticas ocorridas na América do Sul durante o Terciário e Quaternário, que permitiram a formação das savanas decorrentes das oscilações do clima, e possivelmente o regime de incêndios teve uma contribuição importante (PINHEIRO; MONTEIRO, 2010; SIMON; PENNINGTON, 2012). Evidências florísticas e filogenéticas sugerem que as espécies do Cerrado são derivadas de várias linhagens independentes de famílias de plantas distintas originárias de outras fitofisionomias, com surgimento estimado para o Mioceno (SIMON; PENNINGTON, 2012). Outro fator bastante importante que caracteriza o Cerrado é o sistema complexo de interações entre diferentes ecossistemas e as relações ecológicas presentes entre os diversos táxons que carregam uma forte característica evolutiva e são fundamentais para a manutenção do ecossistema, regendo inclusive o desenvolvimento de diversas plantas (e.g., caninos nativos e insetos polinizadores) (DUTRA E SILVA, 2020).

O sistema biogeográfico do Cerrado é um dos mais antigos, surgindo nos planaltos centrais da América do Sul em condições ambientais específicas por volta de 30 a 45 milhões de anos atrás durante o período Cenozóico, apresentando características ambientais semelhantes a fitofisionomia atual no período Holoceno (BACHELET, 2014; BARBOSA, 1996; NEVES; CORDANI, 1991). A sazonalidade ambiental característica do Cerrado se desenvolveu dentro de um padrão climático densamente sedimentado desde o início do Pleistoceno (AB’SÁBER, 2000). A temperatura apresenta variações entre 40º C no verão e 0º C no inverno (podendo inclusive ocorrer geadas) ao longo do ano, apresentando uma média de 24 ºC e a concentração das chuvas ocorre entre os meses de outubro e abril, com média anual do índice pluviométrico de aproximadamente 1.300 mm a 1.700 mm, e após esse período a umidade do ar é reduzida entre 15% e 30% devido a redução das chuvas e aumento das temperaturas (DUTRA E SILVA, 2020).

A fitofisionomia de savana característica do Cerrado é propensa a ocorrência de incêndios naturais (principalmente entre os meses de agosto e setembro), fazendo parte do processo ecológico e sendo responsável pela manutenção do ecossistema ao interferir positivamente na fauna e na flora adaptadas aos ciclos induzidos pelos incêndios (GOMES; MIRANDA; BUSTAMANTE, 2018; SIMON; PENNINGTON, 2012). A presença de cascas grossas e da alta densidade de biomassa subterrânea das plantas são características decorrentes do processo evolutivo como forma de adaptação aos solos pobres em nutrientes, à seca e ao fogo, tendo sua possível origem adaptativa ainda durante o período de expansão das gramíneas nas savanas tropicais (DANTAS; PAUSAS, 2020; SIMON et al., 2009; SIMON; PENNINGTON, 2012).

O Cerrado é a savana tropical mais diversa do mundo, sendo considerado um hotspost mundial de biodiversidade, com aproximadamente 12.000 espécies de plantas vasculares e apresentando 44% de sua flora endêmica, além de elevada riqueza de espécies em outros grupos como mamíferos, aves, répteis, anfíbios e peixes (FERREIRA et al., 2017; KLINK; MACHADO, 2005). A vegetação de savana apresenta grande variação de composição, com estrutura de mosaico, contendo um elevado número de espécies mesmo em áreas consideradas pequenas, além de alta rotatividade de espécies (AMARAL et al., 2017; DANTAS; BATALHA, 2011; SILVA-MORAES; CORDEIRO; FIGUEIREDO, 2018).

2.4 A FITOFISIONOMIA DOS CAMPOS RUPESTRES

2.4.1 Formação e características

Os campos rupestres fazem parte do domínio do Cerrado e apresentam um complexo vegetacional neotropical majoritariamente arbustivo e herbáceo bastante heterogêneo, formando um mosaico fitofisiomorfológico em áreas montanhosas acima de 900 m de altitude, permeado por afloramentos rochosos de quartzito, arenito ou rocha ferruginosa e solos caracteristicamente arenosos, ácidos, rasos (raramente alcançando três metros de profundidade) e pobres em nutrientes (ALVES et al., 2014; FERNANDES et al., 2018; VASCONCELOS, 2011). A insularidade vegetacional marcante dos campos rupestres é decorrente do histórico da flora local e mesmo em áreas geograficamente próximas a composição florística de diferentes localidades é bastante distinta, ainda que exista similaridades de fisionomias, microclimas e substratos (ALVES; KOLBEK, 2010; PRANCE, 1994). Devido a presença de filtros ambientais severos, características funcionais que permitissem a perpetuação das espécies de plantas foram preservadas ao longo da evolução tais como estratégias especializadas para aquisição de nutrientes, desenvolvimento mais lento, limitação da dispersão e baixo índice de fecundidade (DAYRELL et al., 2018; LE STRADIC et al., 2018; NEGREIROS et al., 2014; OLIVEIRA et al., 2016).

Inicialmente Sampaio (1938) definiu a vegetação arbustiva e herbácea estabelecidas em solos litólicos e afloramentos rochosos de áreas montanhosas como campos alpinos. Diversos autores posteriormente passaram a denominar esse ambiente como savanas de altitude, campo de altitude, campo quartzítico, campo sujo, campo limpo, cerrado rupestre, entre outros, entretanto, alguns desses termos não tiveram sua circunscrição detalhada (ALVES et al., 2014; RIZZINI, 1979; VASCONCELOS, 2011). Magalhães (1966) foi quem definiu o termo campos rupestres em substituição aos outros termos destinados à vegetação características das áreas montanhosas brasileiras, ganhando destaque e ampliação de uso em trabalhos científicos nos anos posteriores. Foram os trabalhos de Giulietti e Pirani (1988) e Giulietti (1997) que contribuíram para uma melhor circunscrição dos campos rupestres e maior destaque para esse ambiente, embora o foco tenha sido a Cadeia do Espinhaço. Foi com o trabalho de Alves et al. (2014) que os campos rupestres foram circunscritos de forma mais direta e precisa, descrevendo os limites geográficos e características ambientais e de vegetação.

A principal representação dos campos rupestres está na Cadeia do Espinhaço, entretanto, a circunscrição deste tipo vegetacional é motivo de estudo e debate entre diversos autores, inclusive sobre a sua presença em áreas montanhosas disjuntas como a Serra da Canastra, serras de Goiás (e.g., Chapada dos Veadeiros), serras de Tocantins (e.g., Parque Estadual do Jalapão), Pará (Serra dos Carajás) e até mesmo no Planalto Residual do Urucum próximo à fronteira do Mato Grosso do Sul com a Bolívia (BARRES et al., 2019; NEVES et al., 2018; VASCONCELOS, 2011; VIANA et al., 2016). Os campos rupestres sofrem influência no sudeste da parte mais ocidental da Mata Atlântica no estado de Minas Gerais, ao norte e oeste são encontrados em meio ao Cerrado e na Bahia estão presentes no semi-árido da Caatinga (ZAPPI et al., 2019).

Os campos rupestres possuem origem de ambientes antigos geologicamente que sofreram processos massivos de intemperismo, erosões, falhas e dobras, sendo posteriormente soerguidas por eventos tectônicos, e constituídos principalmente por afloramentos rochosos que possuem origem metamórfica decorrentes de exposição de rochas quartzíticas pré-cambrianas desde o período Terciário, assim como presença de hematita (rocha ferruginosa) (ALVES et al., 2014; FERNANDES et al., 2018; SCHAEFER et al., 2015). Apresentam precipitação anual acima de 800–1500 mm, com até cinco meses de duração da estação seca e variações consideráveis de temperatura ao longo do dia (ALVES et al., 2014). Em solos de campos rupestres, a mineralização da matéria orgânica é baixa em decorrência do baixo pH e saturação de água durante o verão e há uma menor velocidade de decomposição de matéria orgânica em solos arenosos, ácidos e com ausência de argila e silte (ALVES et al., 2014; BENITES et al., 2003, 2007; SILVA et al., 2004).

Estudos em campos rupestres ferruginosos, por vezes denominados vegetação de canga, mostraram através de análises de solo por meio de isótopos geocronológicos e cosmogênicos que os processos de intemperismo que originaram a canga ocorrem de forma contínua desde ~65 Ma (MONTEIRO; VASCONCELOS; FARLEY, 2018; VASCONCELOS; CARMO, 2018). Os campos rupestres ferruginosos possuem uma característica geoedáfica específica e são compostos por espécies metalófilas (tolerantes a solos pobres em nutrientes, com baixa retenção de água e concentração elevada de metais) que geralmente apresentam em seus tecidos um gradiente elevado de metais pesados que provocam alterações metabólicas e fisiológicas, influenciando diretamente o índice de endemismo nestas áreas, pois, as espécies acabam se tornando especialistas destas condições ambientais (CARMO; JACOBI, 2013; PORTO; DA SILVA, 1989; RIZZINI, 1979; SCHAEFER et al., 2015; SILVA; SECCO; LOBO, 1996).

As mudanças climáticas que ocorreram durante o Pleistoceno funcionaram como um importante condutor para a diversificação de várias linhagens de plantas em campos rupestres, consideradas como importantes áreas OCBIL na América do Sul, criando ilhas altitudinais isoladas em meio a uma matriz contínua de vegetação em áreas mais baixas que promoveram uma diversificação rápida e geograficamente estruturada (BARRES et al., 2019; VASCONCELOS et al., 2020). Durante os períodos interglaciais do Pleistoceno, os campos rupestres atuaram como microrefúgio para espécies adaptadas ao frio e à seca em áreas tropicais durante os ciclos de expansão e retração da vegetação decorrente das mudanças climáticas do Quaternário, impulsionando os níveis atuais de estrutura populacional e diversidade nesse tipo vegetacional (BARBOSA, 2011; BONATELLI et al., 2014; COLLEVATTI et al., 2012). Entretanto, Rapini et al. 2021 defendem que a diversificação em campos rupestres é decorrente de diversos fatores em diferentes escalas de tempo e que a hipótese de refúgio do Pleistoceno é bastante superestimada por defender que a mudança climática desse período é a variável responsável pela elevada diversidade de espécies em campos rupestres.

Análises biogeográficas e filogenéticas mostraram que a flora da canga de Carajás forma um grupo coeso e distinto da flora em canga ou quartzito do leste do Brasil, além de identificar que, apesar da hiperdiversidade, a canga presente no Quadrilátero ferrífero é mais similar aos campos rupestres quartizíticos presentes no restante da Cadeia do Espinhaço do que a flora da canga amazônica de Carajás, corroborado pela perspectiva filogenética ao revelar que certas linhagens em nós mais profundos apresentaram padrões de associação com substratos específicos (ZAPPI et al., 2019). A vegetação é majoritariamente herbácea e arbustiva, principalmente com espécies terófitas, geófitas e pequenas fanerófitas (sendo a família Asteraceae uma das mais ricas), e a presença de tipos de hábitos está bastante associada à concentração de sinúsias em tipos estruturais de canga distintos, criando uma variabilidade fisionômica marcante decorrente das características geomorfológicas e topográficas (CARMO; JACOBI, 2013; GAGEN et al., 2019; MOURÃO; STEHMANN, 2007; VIANA; LOMBARDI, 2007). A elevada diversidade alfa e beta é uma característica marcante em áreas elevadas de canga, além da diferença na composição de angiospermas entre ambientes de arenito (bastante presente na Cadeia do Espinhaço) e afloramentos ferruginosos de canga (e.g., Solanaceae e

Verbenaceae são mais abundantes em canga, enquanto que Eriocaulacea e Xyridaceae são menos abundantes nesse ambiente) (JACOBI; CARMOS, 2008; SKIRYCZ et al., 2014).

Evidências indicam que a canga é mais porosa comparada ao solo raso e rochoso presente nos campos rupestres quartzíticos e o solo laterítico com lençol freático encontrado no cerrado, possuindo a capacidade de armazenar água por períodos de tempo duradouros (MOTA, N. et al., 2018). As variações encontradas na concentração de nutrientes na serapilheira, vegetação e solo dos ecossistemas de canga pode ser explicado pela especificidade da ciclagem de N, dinâmica dos nutrientes e disponibilidade de água entre as fisionomias (MITRE et al., 2018). Utilizando critérios de constituição do solo e distribuição de espécies, alguns autores defendem que a canga não é um ambiente uniforme (e.g., canga couraçada e canga nodular), inclusive cangas de diferentes locais apresentam condições climáticas distintas (e.g., Quadrilátero Ferrífero é Cwb-clima subtropical de altitude, enquanto que Carajás é Awi- clima tropical chuvoso com seca de inverno) (MOURÃO; STEHMANN, 2007; RIZZINI, 1979; SKIRYCZ et al., 2014).

2.4.2 Endemismo e riqueza de espécies

O ambiente único e rico em espécies endêmicas atraiu a atenção de diversos pesquisadores desde o século XIX, com presença de importantes nomes no cenário científico tais como Langsdorff, Saint-Hilaire e Lund (FERNANDES et al., 2016; MÜGGE et al., 2016). Ao longo dos últimos 50 anos diversas novas espécies foram descritas para os campos rupestres, principalmente com a intensificação das pesquisas de catalogação da biodiversidade iniciada na década de 1960 (FERNANDES et al., 2018). Muitas espécies possuem distribuição restrita a uma determinada localidade e em diversos casos formam comunidades de espécies especialistas deste microambiente, fortalecendo a dissimilaridade florística entre montanhas distintas (ALVES et al., 2014). O elevado índice de endemismo e riqueza de espécies pode ter sofrido grande influência de microrefúgios interglaciais, favorecendo a intensificação de microclimas em um ambiente diverso e consequente redução de extinções (BARBOSA; FERNANDES; SANCHEZ-AZOFEIFA, 2015).

A diversidade de espécies é comparável aos ambientes florestais em termos de número de espécies e supera proporcionalmente em quantidade de espécies ameaçadas (FERNANDES et al., 2018). A composição das espécies vegetais nos campos rupestres é bastante heterogênea, apresentando elevada diversidade alfa e beta (ABRAHÃO et al., 2019). Os campos rupestres abrigam mais de 5000 espécies de plantas vasculares em uma área de aproximadamente 66.000 km^2, sendo um dos maiores centros de endemismo do mundo (SILVEIRA et al., 2016).

Estimativas indicam que 17% da biodiversidade botânica pertence a menos de 1% do território brasileiro, representado pelos campos rupestres (FERNANDES et al., 2016). Dentre as Angiospermas, Asteraceae, Eriocaulaceae, Melastomataceae, Velloziaceae e Xyridaceae estão entre as famílias mais bem representadas em campos rupestres, apresentando uma grande riqueza de espécies e elevado índice de endemismo (ALCANTARA; REE; MELLO-SILVA, 2018; COLLI-SILVA; VASCONCELOS; PIRANI, 2019; MATTOS et al., 2019; MONTEIRO et al., 2021; ZAPPI et al., 2019).

A baixa disponibilidade de nutrientes e concentrações de minerais no solo juntamente com a variabilidade climática associada ao gradiente altitudinal e sazonalidade marcante, formam um arcabouço de filtros ambientais com grande influência nos elevados índices de diversidade e endemismo (FERNANDES et al., 2018; NEGREIROS et al., 2014). Devido ao mosaico de tipos de solo (especialmente pobres em P e N), há uma pressão ambiental que favorece a seleção e prevalecimento de características (e.g., raízes especializadas para maior eficiência na aquisição de nutrientes) que tornam as espécies botânicas especialistas em condições específicas de nutrientes do solo em uma escala espacial muito pequena, gerando um aumento da diversidade local (ABRAHÃO et al., 2019).

Além das condições de solo adversas, outros fatores que podem explicar a baixa riqueza e diversidade em locais mais elevados de campos rupestres são as baixas temperaturas, grande amplitude térmica diurna e exposição ao vento, que impedem o estabelecimento de um grande número de espécies (FERNANDES et al., 2016; MOTA, G. et al., 2018). O caráter de mosaico conferido a este tipo de vegetação é decorrente principalmente do conjunto de comunidades herbáceo-arbustivas que variam de acordo com o relevo, substrato, microclima e profundidade do solo, sendo também uma das explicações da grande diversidade encontrada ao longo do gradiente altitudinal (MOTA, G. et al., 2018).

Apesar das diferenças pedológicas existentes em áreas de campos rupestres rochosas e arenosas, a vegetação apresenta uma rápida recuperação da biomassa após os incêndios, com variação não significativa na riqueza de espécies em solos arenosos após a ação do fogo e maior riqueza de espécies em solos rochosos apenas logo após a recente queimada, e essa ausência de mudança na composição das comunidades botânicas em resposta ao fogo pode ser explicada pela elevada heterogeneidade da vegetação do campo rupestre (LE STRADIC et al., 2018). Espécies de campos rupestres possuem um sistema subterrâneo (responsável por mais de 50% da biomassa) bastante desenvolvido, com presença de estruturas de armazenamento e que favorecem a resiliência de mudas contra incêndios e períodos mais áridos (ALVES et al., 2014; ALVES; KOLBEK, 2010).

A família Asteraceae em campos rupestres apresenta padrões de composição de comunidades com baixa similaridade florística mesmo entre locais próximos, elevada diversidade, distribuição geográfica restrita e micro-endemismos, sendo a variabilidade do relevo e as características edáficas (e.g., textura e fertilidade do solo) as variáveis que mais influenciam a composição e abundância das espécies (CAMPOS et al., 2019; CHAVES et al., 2019a). Por ser uma área OCBIL, as condições climáticas associadas a outras variáveis (especialmente referentes ao solo) possuem forte influência na distribuição de Asteraceae em campos rupestres, principalmente considerando as projeções de drásticas reduções desse tipo vegetacional (CAMPOS et al., 2019; CHAVES et al., 2019b). Em campos rupestres da Cadeia do Espinhaço, a família apresenta uma grande riqueza de espécies principalmente no Espinhaço Meridional, entretanto, poucas espécies estão protegidas em unidades de conservação, o que, a longo prazo, pode acarretar em perdas significativas de diversidade nesta fitofisionomia, já que Asteraceae pode ser considerada uma família modelo em planejamento de conservação por ser umas das maiores famílias de angiospermas e possuir grande representatividade em áreas abertas e montanhosas (CAMPOS et al., 2019; CHAVES et al., 2019a, 2019b).

2.5 CONSERVAÇÃO NO CERRADO E CAMPOS RUPESTRES

A expansão das fronteiras agrícolas e demográficas no Cerrado progrediram desde o final da década de 1930, com ampliação da política de expansão apoiada e incentivada pelo governo federal brasileiro, incluindo a expansão das rodovias e ferrovias que conectaram os principais centros econômicos com a região central do país e a fundação de Brasília no final da década de 1950 (DUTRA E SILVA, 2020). Ainda durante as décadas de 1960 e 1970, subsídios, programas de desenvolvimento e o uso de novas tecnologias foram determinantes para a criação de um ambiente favorável ao agronegócio, impulsionado pelo forte desempenho da economia brasileira decorrente de uma política de desenvolvimento nacional no Cerrado (KLINK et al., 2020).

Apesar do Cerrado abrigar aproximadamente 30% da biodiversidade brasileira, apenas uma pequena parcela de sua cobertura se encontra protegida e menos de 19,8% permanece inalterado (FRANÇOSO et al., 2015; STRASSBURG et al., 2017). Cerca de 40–55% do Cerrado possui alguma intervenção agrícola, por pastagens ou florestas plantadas e apresenta menos de 50% da cobertura vegetal natural remanescente, superando a taxa de desmatamento da Amazônia (BEUCHLE et al., 2015; ESPÍRITO-SANTO et al., 2016; GRECCHI et al., 2014; SANO et al., 2010). As áreas protegidas representam cerca de 8,3% do território do Cerrado e esse percentual reduz para 6,5% quando apenas a vegetação nativa é considerada (FRANÇOSO et al., 2015). Por apresentar uma paisagem altamente heterogênea várias regiões do Cerrado estão sujeitas a severas ameaças, principalmente na transição Cerrado-Amazônia, onde há presença de intenso desmatamento (COLLI; VIEIRA; DIANESE, 2020).

Áreas protegidas que apresentam alta biomassa de árvores com propósito de compensar as emissões de gases de efeito estufa não indicam que possuem uma grande diversidade de espécies, ou seja, não há correlação entre biomassa e diversidade, o que torna difícil a integração entre a conservação da biodiversidade e a redução de emissão de gases (MORANDI et al., 2020). A diversidade genética intraespecífica apresenta menor riqueza genética em áreas ao sul e com elevado índice de desenvolvimento humano, provavelmente em decorrência da perda e fragmentação de habitat, sendo importante uma investigação mais profunda através de estudos genéticos em áreas ao norte do Cerrado e em áreas protegidas para avaliar o manejo das populações e o status de conservação das espécies, pois a diversidade genética constitui um importante papel na adaptação e estabelecimento das espécies nas áreas do Cerrado (BALLESTEROS-MEJIA; LIMA; COLLEVATTI, 2020). Desta forma, diferentes estratégias de conservação do Cerrado em áreas estáveis e instáveis podem ser mais eficientes, aplicando a conservação in situ ao norte, pela capacidade de abrigar maior diversidade genética em áreas naturais remanescentes, e ex situ ao sul, devido a maior densidade demográfica (COLLI; VIEIRA; DIANESE, 2020).

Os efeitos das ações conjuntas do rápido crescimento do agronegócio e desenvolvimento de infraestrutura, da má elaboração e aplicação de leis ambientais e do baixo investimento em pesquisa e conservação geram um grande colapso da biodiversidade no Cerrado (ALVES et al., 2018; FERNANDES et al., 2017; OVERBECK et al., 2018; STRASSBURG et al., 2017). Os impactos ambientais gerados pelos reservatórios hidrelétricos e pela expansão de áreas urbanas são bastante significativos, entretanto, as principais causas do desmatamento do Cerrado são o estabelecimento de pastagens e monoculturas de *commodities* (FRANÇOSO et al., 2015; SANTOS et al., 2021). Estimativas indicam uma perda considerável da biodiversidade do Cerrado nas próximas décadas decorrente principalmente de desmatamento, levando diversas espécies endêmicas a extinção e consequentemente comprometendo os serviços ecossistêmicos (STRASSBURG et al., 2017; VIEIRA; PRESSEY; LOYOLA, 2019). Características importantes do solo como a densidade aparente, o pH e a disponibilidade de P e K são bastante afetadas pela conversão da vegetação natural em áreas de plantio (ZAGO et al., 2018).

O crescimento estimado da produção de soja e cana-de-açúcar pode ser acomodado em áreas agronomicamente mais adequadas que estão atualmente sendo utilizadas como pasto e transferir os centros de criação de gado para outras áreas sem aumentar a conversão do Cerrado em novos pastos, conciliando a expansão da produção agrícola, a conservação do Cerrado remanescente e a restauração de habitats críticos para espécies ameaçadas de extinção (STRASSBURG et al., 2017). Além disso, é importante estabelecer áreas de proteção que possam proteger a biodiversidade de forma efetiva com redução de riscos provocados por mudanças climáticas e utilização antrópica da terra, evitando conflitos de interesse principalmente econômicos e utilizando inclusive programas de manejo incêndios (DURIGAN; RATTER, 2016; OLIVEIRA et al., 2021; VELAZCO et al., 2019; VIEIRA; PRESSEY; LOYOLA, 2019).

O processo de degradação dos campos rupestres tem sua história iniciada ainda no século XVII com a intensa mineração de ouro, havendo posteriormente uma maior dedicação a exploração de pedras preciosas (e.g., diamante) e ao longo das décadas mais recentes a extração de ferro e manganês têm sido o foco da mineração local (FERNANDES et al., 2020). Há uma variedade de atividades que atingem negativamente a biodiversidade dos campos rupestres e a disponibilidade dos serviços ecossistêmicos, destacando o mau planejamento de infraestrutura dos municípios (e.g., construção de estradas e crescimento urbano), mineração descontrolada, ecoturismo inadequado, florestamento com árvores exóticas (e.g., eucaliptos), sobrepastoreio de gado, extração sem manejo de espécies ornamentais e elevada frequência de incêndios de origem antropogênica (BATISTA et al., 2018; FERNANDES et al., 2018; PENA et al., 2017; RIBAS et al., 2016; SILVEIRA et al., 2016).

Menos de 10% das áreas de campos rupestres estão em áreas protegidas, sendo um quantitativo ineficiente na proteção e manutenção da biodiversidade e serviços ecossistêmicos neste tipo vegetacional, entretanto, propostas de estabelecimento de planos de conservação da biodiversidade de forma mais ampla tem surgido recentemente (FERNANDES et al., 2018, 2020; PACHECO; NEVES; FERNANDES, 2018). Fernandes et al. (2020) propõem o Plano de Ação para o Campo Rupestre (Action Plan for the Campo Rupestre – APCR) que envolve medidas de conservação conjunta entre políticas públicas, conservação, manejo e restauração da biodiversidade e serviços ecossistêmicos, implantação de ecoturismo sustentável, planejamento de crescimento socioeconômico, desenvolvimento científico-tecnológico e aumento do engajamento das comunidades locais e científicas, visando o benefício mútuo entre o meio ambiente e a população associados aos campos rupestres.

Áreas protegidas são comumente estabelecidas em locais onde a efetividade da conservação das espécies é baixa, pois prioriza o custo de aquisição da terra em detrimento do valor biológico agregado (FRANÇOSO et al., 2015; VENTER et al., 2014). Em campos rupestres há grupos distintos de composição florística que necessitam de atenção específica para o estabelecimento de áreas protegidas mais amplas nestas diferentes áreas, preenchendo principalmente as diversas lacunas de conservação existentes atualmente (NEVES et al., 2018).

A vulnerabilidade dos campos rupestres aos impactos ambientais decorrentes de invasões de espécies exóticas e crescente pressão extrativista sobre os recursos naturais é potencializada pela grande rotatividade de espécies vegetais encontradas ao longo do gradiente altitudinal e estimativas futuras apontam para uma grande redução de habitat e elevado potencial de extinção de espécies devido as mudanças climáticas (BITENCOURT et al., 2016; MOTA, G. et al., 2018). Embora os índices de endemismo vegetal nos campos rupestres estejam entre os maiores do mundo, esse ambiente apresenta algumas das taxas mais altas de intervenção antrópica de habitat devido às atividades de mineração, turismo e desenvolvimento de infraestrutura, com previsões estimando uma perda significativa de área em cerca de 82% nas próximas décadas, impactando os serviços ecossistêmicos da região (FERNANDES et al., 2018; SILVEIRA et al., 2016).

Através de um plano de conservação para as principais espécies de plantas ameaçadas de extinção no campo rupestre é possível proteger, em média, mais de 25% das áreas de espécies ameaçadas, identificando regiões prioritárias para diferentes ações de conservação através de mapas estratégicos para as tomadas de decisões, favorecendo áreas com frequência intensiva de incêndios e restringindo o manejo da terra a uma área relativamente pequena de apenas 17% da região e evitando locais com agricultura extensiva e mineração (MONTEIRO et al., 2018). O uso do fogo como forma de manejo de conservação de espécies em campos rupestres é uma das ferramentas que pode ser utilizada para manter a dinâmica de reestabelecimento das comunidades de plantas, evitando o empobrecimento biológico (LE STRADIC et al., 2018).

2.6 BIOGEOGRAFIA, FILOGENIA E MODELAGEM DE NICHO

Ao longo dos últimos anos a biogeografia têm se consolidado cada vez mais nos estudos evolutivos, especialmente quando se trata da filogeografia, aplicando diversas metodologias com intuito de compreender a história evolutiva dos grupos taxonômicos, como a modelagem de nicho, diversificações biogeográficas e análises biogeográficas filogenéticas que contribuem para reconstrução da evolução das espécies com base em fatores de alcance geográfico e tolerâncias ecológicas, além de propor modelos que permitem a investigação de processos importantes, tais como interações ecológicas e mudanças climáticas, dentro das inferências biogeográficas (WEN et al., 2013). Em Asteraceae diversos grupos como *Eupatorium*, *Pleurophyllum* e *Artemisia* foram alvos de estudos biogeográficos associados a análises moleculares e filogenéticas para entendimento de seus respectivos processos históricos macroevolutivos (MALIK et al., 2017; SCHMIDT; SCHILLING, 2000; WAGSTAFF; BREITWIESER; ITO, 2011). Recentemente o trabalho de Keeley, Cantley, Gallaher (2021) utilizando análise de reconstrução de área ancestral em árvore datada da tribo Vernonieae (a qual Lychnophorinae pertence) contribuiu para o entendimento do processo de dispersão e diversificação das linhagens dos clados compostos por espécies do Novo Mundo e do Velho Mundo, inclusive corroborando em certos aspectos com estudos prévios.

Além de contribuir para a classificação das espécies em uma perspectiva macroevolutiva por meio do entendimento das relações existentes entre os diferentes táxons, as análises filogenéticas moleculares permitem compreender a história evolutiva e a geração da diversidade dos grupos taxonômicos através do cálculo de estimativas de tempo de divergência (BREMER; WANNTORP, 1978; KIM; KIM, 2018; STEVENS, 1991). Os trabalhos com análises filogenéticas realizadas por Keeley et al. (2007), Loeuille, Keeley, Pirani (2015), Keeley, Cantley, Gallaher (2021) e Siniscalchi et al. (2019) contribuíram de forma bastante significativa para o entendimento das relações existentes dentro da tribo Vernonieae e consequentemente ajudou a entender melhor os caminhos evolutivos da subtribo Lychnophorinae. Através do estudo de Mandel et al. (2019) utilizando método de datação da filogenia de Asteraceae foi possível estimar a origem da família durante o Cretáceo (~83 Ma) na América do Sul, além de identificar subsequentes dispersões pela América do Norte, Ásia e África, juntamente com séries de diversificação explosiva durante o Eoceno, gerando elevadas taxas de diversificação.

Nos estudos sobre evolução, os cálculos das estimativas de divergência na árvore filogenéticas são cruciais para o entendimento do surgimento de determinados grupos e linhagens e dentro das diferentes abordagens as mais utilizadas buscam incorporar a heterogeneidade das taxas (e.g., bayesiano e penalized likelihood) (FOREST, 2009; GUINDON, 2013; RUTSCHMANN, 2006). A calibração é um passo importante nesse processo e pode ser realizada através das datas estimadas de fósseis ou de datas de divergência estimadas de outras filogenias (SHEN et al., 2021; XU et al., 2019). Apesar disso diversos autores chamam a atenção para o grau de incerteza existente que pode comprometer as interpretações evolutivas (BAELE et al., 2012; BROWN; SMITH, 2018; FOREST, 2009; LEE; OLIVER; HUTCHINSON, 2009; RANGEL et al., 2015).

A reconstrução de estado ancestral tem sido empregada em estudos evolutivos para entender a evolução dos grupos alvos das pesquisas e tem por objetivo estimar valores para um determinado estado ou característica ao longo da topologia de uma árvore filogenética, geralmente nos pontos de cladogênese, possuindo aplicação em áreas como evolução de nicho, biogeografia e evolução molecular (LITSIOS; SALAMIN, 2012; OMLAND, 1999). Essa metodologia é amplamente utilizada nos estudos evolutivos de angiospermas, especialmente para compreender a evolução de características florais e do tamanho do genoma (ENDRESS; DOYLE, 2009; REYES et al., 2018; SOLTIS et al., 2003). Em Asteraceae, os principais trabalhos que empregam a reconstrução de estado ancestral possuem um foco maior nas principais características morfológicas do grupo (e.g., capítulo, hábito e componentes florais) e aspectos reprodutivos (e.g., autoincompatibilidade e autocompatibilidade), buscando entender como tais características influenciaram a evolução da família através da identificação das estimativas das características ancestrais (FERRER; GOOD-AVILA, 2007; PANERO et al., 2014).

Realizar o cálculo de sinal filogenético é uma importante etapa dos estudos em evolução, pois, é através deste teste que é possível estimar a tendência de certas espécies possuírem maior similaridade entre si, de acordo com certas características, que com outra espécie selecionada aleatoriamente na árvore filogenética (MÜNKEMÜLLER et al., 2012; REVELL; HARMON; COLLAR, 2008). Existem diversos índices que podem ser aplicados, através de abordagens distintas de cálculos, de acordo com os dados analisados, onde um forte sinal filogenético indica que a característica ou nicho é mais conservada, não havendo aleatoriedade no processo evolutivo (LOSOS, 2008; MÜNKEMÜLLER et al., 2012; REVELL; HARMON; COLLAR, 2008). Dentre as principais métricas utilizadas estão o Cmean, K, Moran’s I, Lambda e D (ABOUHEIF, 1999; BLOMBERG; GARLAND; IVES, 2003; FRITZ; PURVIS, 2010; GITTLEMAN; KOT, 1990; PAGEL, 1999).

A modelagem de nicho ecológico é uma ferramenta importante para a predição da distribuição de espécies em diferentes períodos de tempo de acordo com a adequabilidade ambiental e nos últimos anos tem sido utilizada como recurso para fundamentar tomadas de decisões que envolvem estudos de conservação de espécies (FRANS et al., 2021; GUISAN et al., 2013). Apesar da modelagem de nicho ecológico auxiliar a identificar possíveis áreas de distribuição de espécies pouco amostradas, é preciso levar em consideração que a construção dos modelos sofre influência de diversos fatores, como as variáveis preditoras, os dados geográficos de presença e ausência das espécies, correlação espacial, número de espécies e algoritmo utilizado, portanto, tais aspectos precisam ser levados em consideração, especialmente no que tange a decisões em conservação (VELAZCO et al., 2020). Apesar disso, é uma importante ferramenta no auxílio na determinação de Áreas de Proteção Ambiental, inclusive no controle de possíveis ameaças, como atividades antrópicas e espécies invasivas (KARIYAWASAM; KUMAR; RATNAYAKE, 2019; VELAZCO et al., 2020). A utilização da modelagem de nicho ecológico é especialmente importante no controle da dinâmica de expansão e contração das distribuições das espécies em áreas protegidas decorrente de ameaças ou até mesmo consequência do sucesso no manejo e práticas de conservação (FRANS et al., 2021; PETERSON; ROBINS, 2003).

Uma outra importante ferramenta é a análise de lacuna (gap analysis) que tem por objetivo identificar áreas com ausência de proteção de biodiversidade e que necessitam de maior atenção em planos que buscam aplicar medidas de conservação (SHARAFI et al., 2012; VAN BREUGEL et al., 2015). A análise de lacuna tem sido bastante utilizada para avaliar áreas prioritárias para aplicação de políticas de proteção ambiental com base no status de conservação das áreas analisadas, comumente seguindo critérios de mudanças ambientais, perda de habitat e mudanças climáticas (OLDFIELD et al., 2004; SHARAFI et al., 2012). É possível aplicar a análise através de diferentes abordagens, incluindo estudos de habitat (e.g., modelagem de nicho), diversidade genética e distribuição e riqueza de espécies (MAXTED et al., 2008; SHARAFI et al., 2012).

3 ARTIGO 1 – THE MACROEVOLUTIONARY ROUTE OF THE SUBTRIBE LYCHNOPHORINAE (ASTERACEAE: VERNONIEAE)[1]

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Shortened title: Macroevolution of the Subtribe Lychnophorinae

Abstract

Premise of the Research: This research was undertaken to describe the processes that influenced the macroevolutionary history of the subtribe Lychnophorinae. This can help to comprehend the evolutionary mechanisms and key morphological characters that influenced the species diversification in the Cerrado domain. Furthermore, this investigation contributes to better understand lineage speciation in *campos rupestres* and biogeographical processes in the Espinhaço range.

Methodology: We reconstructed and dated the Lychnophorinae phylogenetic tree through maximum likelihood and penalised likelihood, respectively. We selected the most representative morphological characters of the subtribe (habit, bladder-like trichome, leaf sheath, syncephalia, number of florets per head, pappus series, pappus type and pappus duration), executed ancestral state reconstruction using the Markov model and calculated phylogenetic signal through the D statistic. Additionally, we selected a biogeographical model to estimate the ancestral ranges in each clade through the DEC, DIVALIKE and BAYAREALIKE models with addition of dispersal funder event and dispersal by range parameters.

Pivotal Results: Lychnophorinae emerged during the Miocene and a greater number of lineages appeared during the Pleistocene. Most of the selected character states present in the genera nowadays also established during the Pleistocene. Estimates of ancestral area range

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demonstrate a possible effect of contraction and expansion of ancestral species distributions, as well as showing the origin of the group in the Espinhaço Range. Furthermore, dispersal events by founder effect, mainly from the Espinhaço Meridional, were predominant processes in the biogeographic history of the group.

Conclusions: The Lychnophorinae subtribe emerged in the Espinhaço Range during the Miocene, passing through several climatic oscillations and consequently contracting and expanding lineage distributions. Dispersal founder events associated with important morphological characters (treelet habit, amplexicaul leaf sheath and setose pappus), contributed to the subtribe distribution expansion, helping species to colonize other ecological niches, especially towards the end of Pleistocene.

Keywords: ancestral range estimate, ancestral state reconstruction, BioGeoBEARS, biogeography, campos rupestres, phylogenetic dating

Introduction

Angiosperms represent about 90% of plant species in terrestrial environments and the group diversification process was marked by an accelerated increase in the abundance, diversity and distribution of various lineages during the Late Cretaceous (100–66 Ma), with most families diverging in this period and diversifying during the Cenozoic (Friis et al. 2011; Hernández-Hernández and Wiens 2020; Ramírez-Barahona et al. 2020). Climate changes initiated in the Eocene-Oligocene transition period (34 Ma) intensified along the Middle Miocene (15 Ma), causing a global cooling and an increase in the aridification process in several places, which promoted the advance of dry environments and disrupted important intercontinental routes composed of forests (Folk et al. 2020).

However, tropical forests suffered fewer extinctions when compared to temperate habitats, harbouring the oldest angiosperm families and showing higher rates of diversification (Igea and Tanentzap 2020; Ramírez-Barahona et al. 2020). The possible explanations of the high rates of diversification in angiosperm families are the low extinction rates in widely distributed lineages and great fragmentation followed by habitat specialization, thus, increasing the probability of emergence of key innovations that allow species to colonize other areas and expand their niche and geographic distribution (Vamosi and Vamosi 2011; Hernández-Hernández and Wiens 2020).

The diversification of endemic lineages of the Espinhaço Range dates back to the last major tectonic events in Cretaceous period and, according to Pleistocene Refuge Hypothesis (PRH), intensified significantly during the Pleistocene period as a consequence of the climatic fluctuations, favouring the emergence of climatically stable areas in Espinhaço Range that acted as an important catalyst for the diversification of *campos rupestres* flora (Dussin and Dussin 1995; Ribeiro et al. 2014; Alcantara et al. 2018a; Barres et al. 2019; Vasconcelos et al. 2020). However, there is evidence of important diversification events in *campos rupestres* in periods before the Pleistocene such as the Miocene or Oligocene (Antonelli et al. 2010; Ribeiro et al. 2014; Alcantara et al. 2018; Fiorini et al. 2019). Although the Pliocene (5 Ma) and Quaternary (2.6 Ma) periods are quite important for the increase in angiosperm species numbers, the increase in diversification resulting from Pleistocene climatic fluctuations in *campos rupestres* remains under debate (Rapini et al. 2021).

Species distribution in disjunct areas are common in several mountainous environments and biogeographic studies based on dated plant phylogenies occurring in *campos rupestres* suggest that the most plausible explanation for the disjunct distributions of several plant lineages is vicariance events (Barres et al., 2019; Bonatelli et al., 2014; Fiorini et al., 2019). These disjunct distributions are frequently interpreted as *campos rupestres* interglacial refuges (Collevatti et al. 2009; Bonatelli et al. 2014; Perez et al. 2016; Barres et al. 2019; Fiorini et al. 2019). However, statistically reliable evidence that glacial cycles did not interfere in such disjunctions are provided by the age of the most recent common ancestor of these disjunct lineages as they frequently precede the Last Glacial Maximum (LGM) (Rapini et al. 2021). Therefore, analysing the diversification in *campos rupestres* only from the temporal point of view may not be sufficient to determine the coalescence of the lineages and sustain the PRH (Rapini et al. 2021).

The *campos rupestres* are formed by a phytophysiognomic island system composed of a mostly herbaceous-shrubby vegetation mosaic over rocky outcrops associated with specific edaphic components consisting of quartzite, sandstone and ferruginous rocks in shallow, acidic and nutrient-poor soils (Vasconcelos et al. 2020; Rapini et al. 2021). This vegetation is present mainly in the Espinhaço Range at elevations above 900 m a.s.l., with a high rate of endemism and harbouring about 15% of the Brazilian flora in approximately 1% of the national territory (Fernandes 2016; Silveira et al. 2016; Zappi et al. 2017; Fernandes et al. 2018; Mattos et al. 2019; Silveira et al. 2019). These plant communities are composed of phylogenetically structured lineages, specialized to environmental conditions (mainly edaphic), high ancestral phylogenetic niche conservatism and low dispersive potential (Conceição et al. 2016; Zappi et al. 2017).

Because of the ancient characteristic of the environment, nutrient-poor soils, high diversity and strong climate influence, the *campos rupestres* are recognized as OCBIL (Old, Climatically Buffered, Infertile Landscape) areas, comprising a framework of factors that contribute to the maintenance of diversity and endemism (Mucina and Wardell-Johnson 2011; Oliveira et al. 2015; Conceição et al. 2016; Silveira et al. 2016; Hopper et al. 2021; Silveira et al. 2021). Furthermore, the independent evolutionary processes that occurred by drift or selection in population systems with long historical periods of isolation were favoured by the combination of high specialization, limited seed dispersal (short distance) and climate stability areas present in *campos rupestres* and supported by the OCBIL theory (Hopper et al. 2021; Silveira et al. 2021). Thus, OCBIL areas such as *campos rupestres* present a set of characteristics that makes microhabitats stable during climatic fluctuations, serving as a cradle for recently generated lineages and museums for old lineages that persist during the evolutionary process (Main 1997; Bitencourt and Rapini 2013; Schut et al. 2014).

An important group of the Asteraceae family with several endemic species present in *campos rupestres* is the subtribe Lychnophorinae. Using morphological and molecular data (ETS, ITS, *ndh*F, *rpl*32-*trn*L), phylogenetic studies established the monophyletism of Lychnophorinae and allowed a better understanding of genera relationships, such as the split of the polyphyletic *Lychnophora* s.l. in *Lychnocephalus*, *Lychnophora* s.s. and *Lychnophorella* (Loeuille et al. 2015; Loeuille et al. 2015). The Lychnophorinae subtribe (Asteraceae: Vernonieae) is characterized by woody species with subshrubby to treelet habit, and the caulirosula habit is likely associated with greater protection against fire, protecting the apical meristem (Loeuille et al. 2019). The indumentum is frequently composed of 3–5-armed bladder-like trichomes acting as an important structure of mist water absorption (Eller et al. 2016; Boanares et al. 2019). The leaf sheath is also an important characteristic present in several species of the subtribe and probably useful for water retention (Lusa et al. 2018). The syncephaly is a remarkable characteristic of Lychnophorinae and contributes most likely to effective reproductive success and protection against herbivory, being a putative evolutionary response to ecological (e.g., pollination and predation) and environmental factors (e.g., dispersal) (Loeuille et al. 2015a). The group presents a deciduous to caducous, usually paleaceous pappus with one (uniseriate) or more (biseriate/multiseriate) setae series, and during the evolution of some lineages (e.g., *Piptolepis*) the number of series seems to have increased (Marques et al. 2022). This set of pappus characteristics deviates from the typical persistent biseriate setose pappus found in Vernonieae (Robinson 1999). Variation of pappus duration have probably an impact on dispersal dynamics whereas increased number of series and stiffer setae may indicate a functional shift from dispersal to protection against fruit herbivory (Stuessy and Garver 1996).

Most Lychnophorinae species are endemic to Brazil, distributed in the Cerrado[1] domain (the most species-rich tropical savanna in the world), with some species present in Bolivia (*Centratherum cardenasii*, *Eremanthus mattogrossensis* and *E. rondoniensis*) and a species with a Pantropical distribution (*Centratherum punctatum*) (Loeuille et al. 2019; Alves and Loeuille 2021). The diversity center of the group is found in the Espinhaço Range, where the *campos rupestres* vegetation dominates the environment, favouring the high level of microendemism in taxa restricted to this vegetation type (Echternacht et al. 2011; Loeuille et al. 2019). The Lychnophorinae diversification has probably been influenced by the geographic isolation or selective habitat pressures (Loeuille et al. 2019).

The Espinhaço Meridional, recently recognized as a biogeographic province, has the highest level of Lychnophorinae species richness, including some endemic genera (e.g., *Minasia*) (Colli-Silva et al. 2019; Alves and Loeuille 2021). Although the cerrado lineages show putative adaptations to fire during its evolutionary history, the phylogenetic results indicate that Lychnophorinae dominated the *campos rupestres* before occupying cerrado conditions (Loeuille et al. 2015b; Loeuille et al. 2019). Therefore, structural and physiological characteristics of *campos rupestres* Lychnophorinae that protect them from fire may have to be interpreted as exaptation conditions (Simon and Pennington 2012; Loeuille et al. 2019). Such characteristics are, thus, originally an adaptive response to climatic and edaphic conditions (Simon et al. 2009; Simon and Pennington 2012; Loeuille, Semir, et al. 2015; Loeuille et al. 2019).

One of the important methods of investigating diversification processes that help us understand large-scale evolutionary processes involves calculation of speciation and extinction rates, which provides the possibility to explain the influence of these variables in the lineage diversification through time, using, e.g., functional characteristics or change in lineages (Maddison et al. 2007; Rabosky 2014; May et al. 2016; Condamine et al. 2017). The existing phylogenetic relationships between different lineages that arise as a result of species diversification can be evaluated by calculating the phylogenetic signal, which indicates whether the evolutionary process follows a Brownian evolutionary model (i.e., randomly generated) or

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[1] "Cerrado" (i.e., uppercase) refer to the phytogeographic domain and "cerrado" (i.e., lowercase) to the vegetation type

if it presents a phylogenetic pattern between the lineages (Blomberg and Garland 2002; Blomberg et al. 2003; Wiens and Graham 2005).

The purpose of this work is to explore the macroevolutionary processes that led to the subtribe diversification of Lychnophorinae through an integrative approach using phylogenetic and biogeographic methodologies. In this way, we intend to answer the questions: 1) what are the divergence times throughout the evolution of Lychnophorinae? 2) in what circumstances biogeographic events influenced the cladogenesis processes and consequently the species diversification? 3) how morphological evolution compares to the biogeographical history of the group?

Materials and Methods

Phylogenetic tree and dating

Molecular matrices of four markers (ITS, ETS, *rpl*32-*trn*L-F and *ndh*F) containing 79 species belonging to 17 genera available in TreeBASE II (study number 15373) were used to infer a Lychnophorinae phylogenetic tree through maximum likelihood in RAxML version 8.2.10 software (Stamatakis 2014). The GTR+I+G evolution model applied was determined through jModelTest 2.1.10 v20160303 software (Guindon and Gascuel 2003; Darriba et al. 2012) based in the AIC test (Akaike Information Criterion). The tree was selected after calculating the highest log-likelihood value in 1000 random permutations and the execution of 1000 bootstrap replications served as the basis for calculating the degree of support of the clades. Due to the absence of fossil records described for Lychnophorinae and Vernonieae, it was necessary to use a secondary calibration approach. We used a temporally calibrated Asteraceae tree produced by Mandel et al. (2019), choosing the calibration points on the MRCA (most recent common ancestor) of the *Chresta pacourinoides* clade at the age of 7.8972 Ma and on the MRCA of the *Eremanthus crotonoides* clade at the age of 4.6602 Ma. The phylogenetic tree dating followed the penalized likelihood approach through treePL (Smith and O'Meara 2012), based on the Maurin (2020), using *Chresta pacourinoides* and *Piptocarpha oblonga* as outgroup.

Ancestral State Reconstruction (ASR)

The following characters and their respective states were selected because of their taxonomic importance: habit (candelabriform treelet, caulirosula, shrub, treelet), bladder-like trichome (absent, present), leaf sheath (absent, amplexicaul, pad-like), syncephalia (absent, present), number of florets per head (1, 2-9, 10-60, 100), pappus series (uniseriate, biseriate, multiseriate), pappus type (paleaceous, setose) and pappus duration (caducous, persistent). Detailed explanations of the character sampling and coding are provided in Loeuille (2011). For the definition of floret states, the methodology applied by Loeuille et al. (2015b) was maintained. In order to maintain a taxonomic consistency and avoid possible incongruent results, the following definitions were applied: the subpaleaceous state was incorporated into the paleaceous state; the deciduous state into the caducous state; *Gorceixia decurrens* has a unique pappus type described as coroniform, in the present study it was specified as paleaceous; *Lychnophora damazioi* has a leaf sheath similar to a pad-like (but non-homologous to the pad-like found in *Piptolepis* and *Lychnophorella*), however, it was classified here as pad-like. Furthermore, the semi-amplexicaul state has been incorporated into the amplexicaul.

The ASRs of each character were performed using the ‘castor’ package (Louca and Doebeli 2018) in the R platform (R Core Team 2020) with the Markov model using the “asr_mk_model” and “hsp_mk_model” functions. All available rate models were applied, being the “ER” for equal rates model; “SYM” which the transition rate i–>j is equal to transition rate j–>i; “SUEDE” with only stepwise transitions i–>i+1 and i–>i-1 allowed, all ‘up’ transitions are equal, all ‘down’ transitions are equal; “SRD” with only stepwise transitions i–>i+1 and i–>i-1 allowed and each rate can be different; and “ARD” which all rates can be different. The best model for each character was selected according to the AIC values.

Phylogenetic signal

The phylogenetic signal of each morphological character was assessed calculating the D statistic (Fritz and Purvis 2010) using the “phylo.d” function from the ‘caper’ package (Orme 2018) in R. This test is based on the assumption of evolution of the character under the Brownian movement. Values of $D \approx 0$ indicate a strong phylogenetic signal (suggests that the trait evolves under a Brownian evolution model), $D \approx 1$ does not imply a phylogenetic signal (suggests that the trait evolves following a random model), $D < 0$ indicates that, under the Brownian model, the trait is phylogenetically more conserved than expected. Significance was assessed by shuffling the characters values between the taxa (10,000 permutations) and *p* values were calculated by comparison with a random null expectation and the predictions of a Brownian model.

Ancestral Range Estimate (ARE)

The ARE analysis was performed using the ‘BioGeoBEARS’ package (Matzke 2014). In order to test which biogeographic processes best explain the current Lychnophorinae species distribution within a historical-macroevolutionary perspective, the vicariance and dispersion events were identified within a stochastic mapping. The selected areas to carry out the biogeographic analyses was based in the Lychnophorinae biogeographic patterns defined by Alves and Loeuille (2021) and took into account the main distribution areas included in the total distribution of subtribe species. The selected areas were: Brasília Arc (BA), Caatinga (Ca), cerrado (Ce), Chapada diamantina (CD), Espinhaço Meridional (EM), Espinhaço Septentrional (ES), Restinga (Re) and Ceará (Cer) (for more detailed information, see Alves and Loeuille (2021)). Three base models were used: DEC (dispersal-extinction-cladogenesis), DIVALIKE (dispersal-vicariance analysis with maximum likelihood implementation) and BAYAREALIKE (bayesian inference for discrete areas with maximum likelihood implementation), due to their wide and solid uses in studies of biogeography (Ronquist 1997; Ree et al. 2005; Ree and Smith 2008; Landis et al. 2013).

The DEC model applies dispersion as a process of expansion (through reach) and extinction as a process of anagenetic contraction. Thus, there is a modification in the geographic variation in the cladogenesis process of the DEC model, defining equal weights for each sympatry event, sympatry by subset and vicariance. The DIVALIKE model has anagenetic procedures similar to the DEC model, however, in a situation where the wide distribution is present in both descendants it does not use sympatry by subsets and makes use of vicariance. In the BAYAREALIKE model, even though the ancestral range is present in many areas, this range is transmitted to the two descendants, so the geographic range does not change during cladogenesis. To represent the founder event (J) speciation within the group, the DEC+J, DIVALIKE+J and BAYAREALIKE+J models were used (Matzke 2014). For each of the previous models (base models with/without the founder event parameter) a distance parameter (X) was added to estimate the effect of geographic distance on dispersion, generating the DEC+X, DEC+J+X, DIVALIKE+X, DIVALIKE+J+X, BAYAREALIKE+X, BAYAREALIKE+J+X models (van Dam and Matzke 2016). After generating the final models, they were submitted to the AIC statistical test to select the model that best represents the biogeographical history of Lychnophorinae. To estimate the quantity and types of anagenetic and cladogenetic biogeographic events in the best model, 1000 biogeographical stochastic mapping (BSM) were simulated (Dupin et al. 2017).

Results

Phylogenetic analyses

The phylogenetic tree inferred by maximum likelihood is congruent with the previous phylogenetic hypotheses (Loeuille et al. 2015b), but with internal relationships better resolved, especially within the *Lychnocephalus* clade. Most clades showed high bootstrap support values (BSS), especially *Eremanthus* (BSS = 100%), *Heterocoma* (BSS = 100%), *Lychnocephalus* (BSS = 100%), *Lychnophora* (BSS = 97%), *Lychnophorella* (BSS = 100%), *Minasia* (BSS = 100%), *Piptolepis* (BSS = 100%), *Prestelia* (BSS = 100%) and *Proteopsis* (BSS = 100%) clades. The case of the *Paralychnophora* clade was interesting because it was the only clade of a monophyletic genera that showed low support (BSS = 47%), however, the clade without *Paralychnophora glaziouana* (the sister to the rest of the group) had BSS = 98%.

The estimated Lychnophorinae crown age was 6.00065 Ma (Messinian, age of Miocene epoch), with the respective confidence interval (CI) of 5.6163–6.6745 Ma (fig. 1). The generic-level clades with high BSS had the respective crown ages: *Eremanthus* 0.7563 Ma (CI = 0.6284–2.5259 Ma), *Heterocoma* 0.3895 Ma (CI = 0.3063–1.5652 Ma), *Lychnocephalus* 0.327 Ma (CI = 0.2278–1.4719 Ma), *Lychnophora* 0.5967 Ma (CI = 0.4968–2.8054 Ma), *Lychnophorella* 0.6779 Ma (CI = 0.4951–2.8108 Ma), *Minasia* 0.2598 Ma (CI = 0.177–1.4911 Ma), *Piptolepis* 0.2116 Ma (CI = 0.125–1.4408 Ma), *Prestelia* 0.3831 Ma (CI = 0.2177–2.0778 Ma) and *Proteopsis* 0.1418 Ma (CI = 0.0513–0.6926 Ma). The nodes in the central portion of the tree showed higher CIs in relation to the rest of the phylogeny nodes.

Except for the capitulum with 100 florets, all other character states presented a strong phylogenetic signal (Table 1). The pappus paleaceous, setose and multiseriate, the capitula with 10–60 florets, the habits candelabriform, caulirosula, shrub and treelet, the leaf sheaths amplexicaul and pad-like, as well as its absence, and the bladder-like trichome were the most conserved characters throughout the Lychnophorinae phylogeny. The pappus caducous, persistent, uniseriate and biseriate, the capitula with 1 floret and 2–9 florets and the syncephalum were the characteristics that presented a Brownian evolutionary model. None of the studied character states presented random or overdispersed evolution models.

Some clades are very important to discuss the results and to facilitate the comprehension they are classified by letters and hereafter mentioned as follows: clade A (Lyhnophorinae clade), clade B (*Prestelia* Alliance), clade C (*Maschalostachys mellosilvae*, *Eremanthus arboreus*), clade D (*Lychnophorella*, *Eremanthus*), clade E (*Hololepis*, *Lychnocephalus*), clade F (*Lychnophora damazioi*, *Lychnocephalus*), clade G (*Piptolepis*, *Eremanthus*), clade H (*Lychnophora*, *Eremanthus*), clade I (*Minasia*, *Eremanthus*) and clade J (*Minasia*, *Paralychnophora*).

ASR

All loglikelihood and AIC values calculated in the ASR analysis for each model and morphological character are available in the Table 2.

Habit (fig. A1): Although the MRCA of the clade A presented very similar likelihoods between the states, the most probable state in the subtribe origin was shrub (27.00%). The reconstruction indicates that the caulirosula habit appeared twice independently, in the clade B (33.35%) during the Pliocene and in the clade C (50.32%) during the Pleistocene. The candelabriform habit seems to have appeared twice independently in Pleistocene, one of them in the *Lychnocephalus* MRCA (0.327 Ma, CI = 0.2278–1.4719 Ma) (99.27%) and the other in the MRCA of the clade D (1.1115 Ma, CI = 1.0093–4.2665 Ma) (71.44%), however, for this clade, two transitions were observed to shrub in *Piptolepis* and to treelet habit in *Eremanthus*. The shrub habit also appears to be present (99.85%) in the *Heterocoma* MRCA (0.3895 Ma, CI = 0.3063–1.5652 Ma). The treelet habit was likely present in the *Paralychnophora* MRCA (0.9046 Ma, CI = 0.5501–2.8051 Ma) and twice in the clade of *Eremanthus* (0.6688 Ma and 0.5761 Ma, CI = 0.5829–2.1124 Ma and 0.4672–1.9172 Ma), during the Pleistocene, but the state of its MRCA is unresolved.

Bladder-like trichome (fig. A2): the reconstructions are inconclusive for the older nodes. The presence of the bladder-like trichome may have been present since the origin of the group (52.12%), in Miocene. The first indication of a loss occurred at the end of the Pliocene (2.6994 Ma, CI = 1.5623–4.3797 Ma) in the clade E, however, four more independent losses were observed, in the MRCA of the *Gorceixia decurrens* and *Blanchetia heterotricha* clade (2.4486 Ma, CI = 0.8892–4.0931 Ma) and in the MRCAs of the *Heterocoma* (0.3895 Ma, CI = 0.3063–1.5652 Ma), *Lychnophora* (0.5967 Ma, CI = 0.4968–2.8054 Ma) and *Proteopsis* (0.1418 Ma, CI = 0.0513–0.6926 Ma) clades.

Leaf sheath (fig. 2): The MRCA of the clade A did not have a leaf sheath. The amplexicaul leaf sheath appeared twice independently in the clade F (99.56%) during Calabrian (Pleistocene) and in the clade C (99.31%) during the Pleistocene. Subsequently, the pad-like leaf sheath appeared twice independently from an amplexicaul ancestral state in the MRCAs of *Lychnophorella* (86.88%) and clade G (90.45%), respectively, during the Pleistocene. Secondary loss of the leaf sheath is observed in the MRCA of the clade H (79.96%) at the age of 0.8779 Ma (CI = 0.7906–3.4454 Ma), Pleistocene.

Syncephalium (fig. A3): The reconstruction was inconclusive for the MRCA of the clade A. Syncephalia emerged twice independently in *Lychnocephalus* MRCA (99.40%) in Pleistocene and in the MRCA of the clade C (58.81%) during the Pleistocene. Several losses of syncephaly occurred several times independently in the Pleistocene in *Proteopsis*, *Minasia*, *Heterocoma* and *Piptolepis* clades, and later (Upper Pleistocene) in the MRCA of *Lychnophora hatschbachii* and *L. candelabrum* (0.0416 Ma, CI = 0.0105–0.2414 Ma) and MRCA of *Eremanthus capitatus* and *E. arboreus* (0.1266 Ma, CI = 0.0697–0.4109 Ma). Therefore, there was a trend of loss of the syncephalium in the genera that diversified during the Pleistocene.

Florets (fig. A4): likelihood values at the older nodes did not show a clear division between states, however, capitulum with 10–60 florets seem to have appeared in the clade C (31.44%), during the Pleistocene. The MRCA (1.3488 Ma, CI = 1.1898–4.0501 Ma) of the clade I had likely (61.48%) one floret per head, as well as in the ancestors of *Lychnophora* and *Eremanthus*. Capitula containing 2–9 florets appeared five times independently, in the *Lychnocephalus* MRCA (0.327 Ma, CI = 0.2278–1.4719 Ma) and in the *Paralychnophora* (0.071 Ma, CI = 0.0327–0.4732 Ma), *Lychnophorella* (0.0201 Ma and 0.1062 Ma, CI = 0.0001–0.0346 Ma and 0.0469–0.6766 Ma) and *Lychnophora* (0.1393 Ma, CI = 0.0791–0.7719 Ma) clades. Capitula with 10-60 florets remained in the *Proteopsis*, *Minasia*, *Heterocoma* and *Piptolepis* clades. The only species with 100 florets in capitula is *Proteopsis hermogenesii*, and this state did not appear in the nodes with a conclusive likelihood. Two reversions to capitula with 10–60 florets occurred, one in the MRCA of the clade J (52.22%) and another in *Piptolepis* MRCA (84.53%). Although the capitula with 10–60 florets appeared in early nodes, at some point during the Pleistocene the capitula with one floret emerged and remained in several ancestors. However, the trend was towards a decrease in the number of florets in the capitula, as can be observed in several lineages leading to one floret per head in several species of *Eremanthus* and *Lychnophora*.

Pappus series (fig. 3): the early nodes showed almost equal likelihoods between states and, therefore, there is no state definition in the clade A MRCA. The multiseriate pappus probably appeared twice independently during the Pleistocene in the MRCA of the clade F (0.9825 Ma, CI = 0.7387–3.1247 Ma) (63.13%) and in *Eremanthus* MRCA (0.7563 Ma, CI = 0.6284–2.5259 Ma) (98.37%). The status of states in other ancestral nodes, including the MRCA of generic clades, have very similar values between states, however, the biseriate state is predominant. The likelihoods of the early nodes of the clade D during the Calabrian (Pleistocene) age indicate that the uniseriate pappus was the most probable character state. It is most likely that the number of pappus series has increased throughout the evolution of Lychnophorinae. Possibly biseriate and multiseriate pappus are independent derivations from uniseriate pappus, as in the *Eremanthus* clade where multiseriate pappus is derived from uniseriate pappus.

Pappus type (fig. 4): most nodes found in the phylogeny showed well-defined likelihoods and paleaceous status was likely present in the MRCA of the clade A (54.43%) during Miocene, still appearing in early diverging lineages. However, the setose pappus is derived from the paleaceous pappus, emerging independently at least four times in subtribe history during the Pleistocene, in the *Eremanthus* (0.3043 Ma, CI = 0.2254–1.0259 Ma), *Minasia* (0.2598 Ma, CI = 0.177–1.4911 Ma), *Prestelia* (0.3831 Ma, CI = 0.2177–2.0778 Ma) and *Paralychnophora* (0.1608 Ma, CI = 0.0811–0.8161 Ma) clades. *Heterocoma*, *Lychnocephalus*, *Lychnophora*, *Lychnophorella*, *Piptolepis* and *Proteopsis* clades had their MRCAs maintained with a paleaceous pappus.

Pappus duration (fig. 5): It was not possible to identify the duration of pappus in the early nodes of the phylogeny before the Pleistocene. However, caducous pappus seems to have appeared first in the history of Lychnophorinae in the Pleistocene in the MRCA of clade C (64.96%). Thus, persistent pappus is derived from caducous pappus and appeared at least three times independently, internally in the *Eremanthus* clade (0.6688 Ma, CI = 0.5829–2.1124 Ma) and in the MRCAs of the clade F (0.9825 Ma, CI = 0.7387–3.1247 Ma) and *Minasia* (0.2598 Ma, CI = 0.177–1.4911 Ma), during the Pleistocene. It was possible to observe one reversion to caducous pappus within the *Eremanthus* clade (0.4208 Ma, CI = 0.2814–1.34 Ma), during the Pleistocene.

ARE

The biogeographic model selected among the 12 ARE models tested was the BAYAREALIKE+J+X, with AIC = 425.4269 (the lowest value compared to the other models) and loglikelihood = -208.7135, indicating that there is strong support for biogeographic patterns resulting from widespread sympatry and founder dispersal events (Table 3). The Likelihood Ratio Test (LRT) results demonstrate that the inclusion of the founder event (J) and geographic distance (X) parameters in the models was significantly important in improving the models, corroborated even by the AIC values. The BSM presented an average of 12.92 founder dispersal events and 63.08 widespread sympatric speciation events, totalling 76 biogeographic events (Table 4).

The BA and CD were the areas that received the highest number of cladogenetic founder dispersal events, with 4.27 and 4.19, respectively, followed by EM with 2.41. The BA was the reception area of three EM founder dispersal events and one ES founder dispersal event. The EM presented an average of two founder dispersal events originating from BA. The CD received two founder dispersal events from EM and two founder dispersal events from ES. The areas with the highest number of founder dispersal events origin were EM, ES and BA, with values of 5.98, 2.99 and 2.31, respectively. Founder dispersal events originating in EM and ES reached CD and BA, while those originating in BA reached EM (Table 5).

Most nodes had well-defined likelihood values for ancestral areas, with some more earlier nodes showing greater uncertainty. The estimated ancestral area for the Lychnophorinae crown node is composed of the EM and ES areas (fig. 6). Some posterior lineages showed EM as an ancestral area in the MRCA of some clades, returning to EM and ES and remaining as more present ancestral areas throughout the phylogeny. In some clades of more recent lineages from the Pleistocene, BA appeared as the ancestral area of the MRCA. The ancestral areas in the crown nodes of some clades were: EM for the *Heterocoma*, *Lychnocephalus*, *Minasia* and *Prestelia* MRCAs; EM and ES for the *Lychnophora*, *Paralychnophora*, *Piptolepis* (in the more nested clades with absence of *Piptolepis ericoides* the ancestral area of the MRCA is just EM) and *Proteopsis* MRCAs; CD for *Lychnophorella* MRCA; BA for *Eremanthus* MRCA (the nested clade formed by *Eremanthus mattogrossensis*, *E. cinctus*, *E. goyazensis* and *E. mollis* the ancestral area of the MRCA is composed of BA and Ce). Some species have wider distribution areas than estimated for their respective MRCAs, namely *Albertinia brasiliensis* (CD, ES, BA, Re and Ca), *E. capitatus* (CD, ES, BA, Re and Ca), *E. crotonoides* (EM, BA and

Re), *E. eleagnus* (EM and BA), *E. erythropappus* (EM, BA and Re), *E. glomerulatus* (CD, ES, EM and BA), *E. incanus* (CD, ES and EM), *E. polycephalus* (ES and EM), *E. syncephalus* (EM and BA), *Gorceixia decurrens* (CD, ES, BA, Re and Ca), *Hololepis pedunculata* (EM and BA), *Lychnophora salicifolia* (CD, ES, EM and BA), *L. passerina* (CD, ES and EM), *L. granmogolensis* (CD, ES and EM), *L. ericoides* (CD, ES, EM and BA) and *Paralychnophora reflexauriculata* (CD and Ca). *Lychnophora itacambirensis*, *L. ramosissima* and *Proteopsis hermogenesii* have a distribution area only in ES, while the ancestral area of their respective MRCAs is wider, also reaching EM. Similarly, *Lychnophora diamantinana* has a distribution area in the EM, with the MRCA ancestral area also including the ES. *Eremanthus arboreus* and *Heterocoma erecta* are distributed in Cer and CD, respectively, and such areas are not included in the ancestral range estimate of their MRCAs.

The occupation of the *campos rupestres* by the subtribe Lychnophorinae dates to the origin of the group in the Miocene (6.0065 Ma, CI = 5.6163–6.6745 Ma). The group remained exclusively in this phytophysiognomy until the late Pliocene (2.6994 Ma, CI = 1.5623–4.3797 Ma). At the beginning of the Pleistocene one of the lineages dispersed to the Chapada Diamantina and posteriorly reaching the Caatinga areas further north (2.4486 Ma, CI = 0.8892–4.0931 Ma). The other lineages continued to diversify exclusively in the *campos rupestres* until the Calabrian (Pleistocene). It is during the Pleistocene that two important dispersal events occur: the first one in the *Eremanthus* MRCA (0.7563 Ma, CI = 0.6284–2.5259 Ma) and formalizes the arrival of Lychnophorinae in the cerrado and the second internally in the *Eremanthus* clade for the restinga (0.2573 Ma, CI = 0.1843–0.8188 Ma).

The graphs showing the number of events calculated in each stochastic map and the comparison between the ancestral range probabilities and the mean values probabilities of stochastic maps are available in the figures A6 and A7, respectively.

Discussion

The speciation of the Lychnophorinae subtribe originated in the areas of *campos rupestres* of the Espinhaço Range since the Miocene, being the main phytophysiognomy in the distributions of ancestral and current species. Approximately 3 Ma after its emergence, it is in the Pleistocene that the evolutionary history of Lychnophorinae accelerates, successive speciation events occur at the same time that new morphological characteristics, such as habit treelet, amplexicaul leaf sheath and setose pappus appear and new distribution areas are colonized (caatinga, cerrado and restinga). Most morphological characteristics of the subtribe (e.g., candelabriform and treelet habits, pad-like leaf sheath, capitula with 1 and 2-9 florets, multiseriate, setose and persistent pappus) appear in the Pleistocene. It is important to highlight that the secondary loss observed in the leaf sheath and the reversal to caducous and persistent pappus occurred nearly simultaneously during the Pleistocene.

The setose pappus is the standard pappus type in tribe Vernonieae and, with a better sampling, would probably be the ancestral state of Lychnophorinae. As the paleaceous pappus limits the species dispersion, the possible return to a setose pappus may have helped the dispersion of Lychnophorinae out of the *campos rupestres*, in the same way that it contributed to the dispersion of Vernonieae. For example, setose pappus may have helped some lineages of *Eremanthus* to reach the restinga and the dispersal of some *Paralychnophora* species to caatinga. Therefore, the setose pappus may be a response to an evolutionary selection that extended the dispersal range of certain lineages and permitted the colonization of new environmentally favourable areas.

Most Lychnophorinae genera emerged in the last 2 Ma and this also had possible implications for the permanence of several morphological characteristics, since some of them (e.g., setose pappus and treelet habit) were established in the MRCA of the genera and were maintained by these lineages until now. Thus, the Pleistocene was a crucial period for the emergence of most of the genera currently known in the group. This entire evolutionary process also contributed to the species being able to somehow disperse and colonize environments outside their original phytophysiognomy, the *campos rupestres*. The genus *Eremanthus* was important for the subtribe as it provided the arrival to the cerrado and the restinga in a short geological period.

Most extant plant lineages in *campos rupestres* may have started their diversification in the late Miocene, after the high species turnover during the Cenozoic and the climate cooling that followed the Mid-Miocene, intensified by the Pliocene and Pleistocene rapid and intense glaciation cycles (Antonelli et al. 2010; Hughes et al. 2013; Vasconcelos et al. 2020; Dantas-Queiroz et al. 2020). It is likely that the speciation of Lychnophorinae was, to some extent, influenced by the dynamics of climatic oscillations and these climatic processes, especially during the Pleistocene, contributed to boost the emergence of new lineages. The Pleistocene was an important geological period for several taxonomic groups (e.g., *Barbacenia* and *Diplusodon*) in *campos rupestres*, with the emergence of some lineages (e.g., *Richterago discoidea*) during this period (Inglis and Cavalcanti 2018; Barres et al. 2019; Cabral et al. 2021).

These climatic oscillations may be one factor that helps to explains why a large part of the Lychnophorinae genera emerged in Pleistocene, possibly influenced by climatic variations and the refuge areas present in the Espinhaço Range. These oscillations generated multiple events of range expansions and contractions in *campos rupestres*, which promoted a high rate of speciation in this mountainous environment, creating a species-pump effect which is, especially in naturally fragmented habitats, an important driver for rapid and recent plant diversification in this phytophysiognomy (Alves and Kolbek 1994; Antonelli et al. 2010; Nevado et al. 2018; Flantua et al. 2019). Vasconcelos et al. (2020) also encountered that Lychnophorinae present a high probability of endemic speciation in *campos rupestres* during the Pleistocene.

One of the main characteristic in *campos rupestres* is the landscape heterogeneity and because of the higher concentration of rocky outcrops and lower proportion of C4 grasses seasonal fire tends to be more restricted and less frequent when compared to the surrounding lowlands, thus, the *campos rupestres* may have acted as refuges for more fire-sensitive lineages in contrast to fire-dependent lineages from cerrado (Giulietti et al. 1997; Ribeiro et al. 2014; Conceição et al. 2016; Silveira et al. 2016). Therefore, the *campos rupestres* may have served as a refuge for Lychnophorinae not only as a result of climatic fluctuations, but also because of less frequent fires than the cerrado. This may have favoured the richness and endemism of Lychnophorinae species in the *campos rupestres*.

The majority of cerrado lineages diversified at 5 Ma or less and coincide with the expansion of the C4 grasses (Simon and Pennington 2012). Thus, the cerrado is composed of independent lineages originating from other phytophysiognomies that had a recent diversification, compared to the *campos rupestres* (Simon et al. 2009; Alcantara et al. 2018). The expansion of fire-prone savannas (cerrado) may have created a favourable environment for the dispersal and establishment of more recent lineages of Lychnophorinae beyond the *campos rupestres*, which could be the case of *Eremanthus*. It is important to highlight that, in addition to *Eremanthus* spp., only *Lychnophora ericoides* and *L. salicifolia* have distribution in the cerrado.

It is not clear from the ASR which possible characteristics favoured the arrival of *Lychnophora ericoides* and *L. salicifolia* in the cerrado. There is also no indication that ancestral lineages of those species have occurred in the cerrado, which reinforces the very recent expansion process of the distributions of these species to the cerrado. Both are morphologically similar species, presenting a candelabriform treelet habit with robust branches, and are present in dense populations (Loeuille et al., 2019). It is likely that the candelabriform treelet habit helped these species in the adaptation against fire in the cerrado (this habit presents thick terminal branches), however, other factors such as tolerance to edaphic characteristics and dispersal opportunity possibly have participated in this process. The thick terminal branch is an important morphological characteristic that confers to species more resistance against fire (Simon and Pennington 2012).

The speciation process in subtribe Lychnophorinae was possibly favoured by a set of morphological characteristics associated with the opportunity for the lineages to disperse in favourable period and environment. Some of these morphological characteristics, such as bladder-like trichome, amplexicaul sheath and treelet habit, have possibly contributed to the success of the group in the Cerrado, especially in the *campos rupestres*, during the global aridification process that occurred between the Miocene and Pliocene (Amaral et al. 2021). The Pleistocene was one of the most important epochs for the establishment of endemic species in Espinhaço Range, but also to colonize new environments (Barres et al. 2019; Vasconcelos et al. 2020; Dantas-Queiroz et al. 2020). This is observed, for example, in the clade of *Eremanhus*, one of the largest genera of the Lychnophorinae (24 species) and with some widespread species (e.g., *E. mattogrossensis*) (Loeuille et al. 2019; Alves and Loeuille 2021).

Probably the set of morphological characteristics of the clade, such as the multiseriate pappus and the treelet habit, gave the species the ability to establish in a larger range of niches, allowing their dispersion both west of the cerrado and also along the Espinhaço Range (Alves and Loeuille 2021). The treelet habit may have conferred a protective advantage against fires in the cerrado by having the higher parts of its structure less affected by these events. In addition, the thicker branches may have provided more protection to internal tissues, similar to *Kielmeyera coriacea* (Clusiaceae) (Simon and Pennington 2012). It is possible that to some degree the moisture retained by bladder-like trichome works as an additional protection against fire and also dryness.

It is interesting to note that the caulirosula habit, despite having emerged between the Pliocene and Pleistocene, has remained currently only in *Minasia*, *Prestelia* and *Proteopsis*. With the exception of *Proteopsis*, which also occurs in the Espinhaço Septentrional, all other species of these genera are endemic to the Espinhaço Meridional (Alves and Loeuille 2021). Therefore, it is very likely that the origin of the caulirosula habit occurred in Espinhaço Meridional and was an important feature for the diversification of Lychnophorinae lineages in the *campos rupestres* and contributed to the endemicity of these three genera in the Espinhaço Range. The caulirosula habit is an important feature for protecting the species from extreme environmental conditions, such as fire and abrupt environmental fluctuations (Loeuille et al. 2019).

Syncephaly and the number of florets in the capitula apparently had some correlation during the Lychnophorinae evolution. This is an expected result due to putative biomechanical pathways to build a syncephalium (Claßen-Bockhoff 1996; Harris 1999), and this was possibly important in the speciation process (fig. 7). The decrease in the number of florets in the capitula during the evolution of Lychnophorinae may have been a response to a greater intensification of insect attacks, since fewer florets in capitula and the syncephaly contributes to protection against herbivory (Burtt 1961; Stebbins 1967; Loeuille et al. 2019). The high rate of diversification of several groups of angiosperms in *campos rupestres* in the Pleistocene described by Vasconcelos et al. (2020) may have also favoured insect diversification and a possible increase in herbivorous groups or individuals during this period, intensifying predation. However, some diverging lineages (*Heterocoma*, *Minasia* and *Piptolepis*) with many flowered capitula and not organised into a syncephalium, may have had a competitive advantage against taxa with syncephalium, highlighting a possible high cost of having a syncephalium in a scenario of mild herbivory pressure.

The Lychnophorinae species distributions in the last 6 Ma went through periods of expansion and contraction, apparently due to the climate changes described for this time period. Our results indicate the subtribe likely originates in the Espinhaço Meridional and Setentrional, indicating also that the *campos rupestres* were always an important area for the different lineages during the speciation process (Vasconcelos et al. 2020; Dantas-Queiroz et al. 2020; Alves and Loeuille 2021). The reduction in the ancestral range for the Espinhaço Meridional between approximately 4.8 Ma and 2.7 Ma indicates that this segment of the Espinhaço Range possibly contributed as a refuge area for the most early diverging lineages of the group during the process of aridification and savanna increase, however, it was into this context that an increase in speciation processes occurred in later periods as observed in others plant groups (Barres et al. 2019; Dantas-Queiroz et al. 2020; Amaral et al. 2021; Bitencourt et al. 2021).

Dispersal events had a great impact on the biogeographic history of Lychnophorinae and certainly were an important factor not only for the group's success in the *campos rupestres*, but also in the species distribution. The Espinhaço Meridional was possibly one of the centers of dispersal to other areas such as the cerrado and also contributed to the advancement of other lineages in other blocks of the Espinhaço Range (Espinhaço Septentrional and Chapada Diamantina). Cladogenetic dispersal events to other areas as in the *Eremanhus* and *Lychnophorella* clades may have influenced the speciation processes of these groups and boosted the expansion of the geographical distribution of Lychnophorinae.

Conclusion

The evolutionary history of Lychnophorinae reveals that some morphological features such as the treelet habit and bladder-like trichome may have been the key factor in the success of the subtribe in the Cerrado. The dispersion and establishment in other environments outside the *campos rupestres* where the subtribe originated was certainly favoured by sets of characteristics that helped in this process. The emergence of new morphological characteristics during the Pleistocene contributed to the accelerated speciation and expansion of Lychnophorinae distribution. Climatic oscillations also played an important role in the speciation process, especially in the Pleistocene, and created opportunities for Lychnophorinae lineages to establish themselves in different environments. The climatically stable areas in *campos rupestres* of the Espinhaço Range provided an environment conducive to speciation of the subtribe, which may explain the high richness and endemism of species in this mountain range, also serving as refuge areas for more fire-sensitives lineages. Furthermore, the most likely biogeographic history showed that Lychnophorinae had its origin during the Miocene in the *campos rupestres*, arriving later in the caatinga, cerrado and restinga, showing how important this phytophysiognomy is for the process of speciation and dispersion of the plant species in Brazilian open habitats.

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References

Alcantara S 2018 Accelerated diversification and functional trait evolution in Velloziaceae reveal new insights into the origins of the campos rupestres’ exceptional floristic richness. Annals of Botany 122:165–180.

Alcantara S, RH Ree, R Mello-Silva 2018 Accelerated diversification and functional trait evolution in Velloziaceae reveal new insights into the origins of the campos rupestres' exceptional floristic richness. Annals of Botany 122:165–180.

Alves FVS, BFP Loeuille 2021 Geographic distribution patterns of species of the subtribe Lychnophorinae (Asteraceae: Vernonieae). Rodriguésia 72.

Alves RJ, J Kolbek 1994 Plant species endemism in savanna vegetation on table mountains (Campo Rupestre) in Brazil. Vegetatio 113:125–139.

Amaral DT, I Minhós-Yano, JVM Oliveira, M Romeiro-Brito, IAS Bonatelli, NP Taylor, DC Zappi, EM Moraes, DAR Eaton, FF Franco 2021 Tracking the xeric biomes of South America: The spatiotemporal diversification of Mandacaru cactus. Journal of Biogeography 48:3085–3103.

Antonelli A, CF Verola, C Parisod, ALS Gustafsson 2010 Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). Biological Journal of the Linnean Society 100:597–607.

Barres L, H Batalha-Filho, AS Schnadelbach, N Roque 2019 Pleistocene climatic changes drove dispersal and isolation of Richterago discoidea (Asteraceae), an endemic plant of campos rupestres in the central and eastern Brazilian sky islands. Biological Journal of the Linnean Society 189:132–152.

Bitencourt C, NM Nürk, A Rapini, M Fishbein, AO Simões, DJ Middleton, U Meve, ME Endress, S Liede-Schumann 2021 Evolution of Dispersal, Habit, and Pollination in Africa Pushed Apocynaceae Diversification After the Eocene-Oligocene Climate Transition. Frontiers in Ecology and Evolution 9.

Bitencourt C, A Rapini 2013 Centres of endemism in the espinhaço range: Identifying cradles and museums of asclepiadoideae (apocynaceae). Systematics and Biodiversity 11:525–536.

Blomberg SP, T Garland 2002 Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15:899–910.

Blomberg SP, T Garland, AR Ives 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Boanares D, AR Kozovits, JP Lemos-Filho, RMS Isaias, RRR Solar, AA Duarte, T Vilas-Boas, MGC França 2019 Foliar water-uptake strategies are related to leaf water status and gas exchange in plants from a ferruginous rupestrian field. American Journal of Botany 106:935–942.

Bonatelli IAS, MF Perez, AT Peterson, NP Taylor, DC Zappi, MC Machado, I Koch, AHC Pires, EM Moraes 2014 Interglacial microrefugia and diversification of a cactus species complex: phylogeography and palaeodistributional reconstructions for Pilosocereus aurisetus and allies. Molecular Ecology 23:3044–3063.

Burtt BL 1961 Compositae and the Study of Functional Evolution. Transactions of the Botanical Society of Edinburgh 39:216–232.

Cabral A, F Luebert, R Mello-Silva 2021 Evidence for Middle Miocene origin and morphological evolutionary stasis in a Barbacenia Inselberg clade (Velloziaceae). Molecular Phylogenetics and Evolution 161:107163.

Claßen-Bockhoff R 1996 Functional units beyond the level of the capitulum and cypsela in Compositae. In: Caligari PDS, Hind DJN, editors. Compositae: Biology & Utilization. Proceedings of the International Compositae Conference. Vol. 2. London: Royal Botanic Gardens, Kew. p. 129–160.

Collevatti RG, SG Rabelo, RF Vieira 2009 Phylogeography and disjunct distribution in Lychnophora ericoides (Asteraceae), an endangered cerrado shrub species. Annals of Botany 104:655–664.

Colli-Silva M, TNC Vasconcelos, JR Pirani 2019 Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. Journal of Biogeography 46:1723–1733.

Conceição AA, A Rapini, FF do Carmo, JC Brito, GA Silva, SPS Neves, CM Jacobi 2016 Rupestrian grassland vegetation, diversity, and origin. In: Fernandes GW, editor. Ecology and Conservation of Mountaintop Grasslands in Brazil. Cham: Springer International Publishing. p. 105–128.

Condamine FL, AB Leslie, A Antonelli 2017 Ancient islands acted as refugia and pumps for conifer diversity. Cladistics 33:69–92.

van Dam MH, NJ Matzke 2016 Evaluating the influence of connectivity and distance on biogeographical patterns in the south-western deserts of North America. Journal of Biogeography 43:1514–1532.

Dantas-Queiroz MV, T da C Cacossi, BSS Leal, CJN Chaves, TNC Vasconcelos, L de M Versieux, C Palma-Silva 2020 Underlying microevolutionary processes parallel macroevolutionary patterns in ancient Neotropical Mountains Running title: Microevolutionary processes parallel macroevolutionary patterns. bioRxiv.

Darriba D, GL Taboada, R Doallo, D Posada 2012 JModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9:772.

Dupin J, NJ Matzke, T Särkinen, S Knapp, RG Olmstead, L Bohs, SD Smith 2017 Bayesian estimation of the global biogeographical history of the Solanaceae. Journal of Biogeography 44:887–899.

Dussin IA, TM Dussin 1995 Jul 1 SUPERGRUPO ESPINHAÇO: MODELO DE EVOLUÇÃO GEODINÂMICA. Geonomos.

Echternacht L, M Trovó, CT Oliveira, JR Pirani 2011 Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil. Flora: Morphology, Distribution, Functional Ecology of Plants 206:782–791.

Eller CB, AL Lima, RS Oliveira 2016 Cloud forest trees with higher foliar water uptake capacity and anisohydric behavior are more vulnerable to drought and climate change. New Phytologist 211:489–501.

Fernandes GW 2016 The Megadiverse Rupestrian Grassland. In: Ecology and Conservation of Mountaintop grasslands in Brazil. Cham: Springer International Publishing. p. 3–14.

Fernandes GW, NPU Barbosa, B Alberton, A Barbieri, R Dirzo, F Goulart, TJ Guerra, LPC Morellato, RRC Solar 2018 The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation 27:2587–2603.

Fiorini CF, MD Miranda, V Silva-Pereira, AR Barbosa, U de Oliveira, LHY Kamino, NFDO Mota, PL Viana, EL Borba 2019 The phylogeography of Vellozia auriculata (Velloziaceae) supports low zygotic gene flow and local population persistence in the campo rupestre, a Neotropical OCBIL. Botanical Journal of the Linnean Society 191:381–398.

Flantua SGA, A O’Dea, RE Onstein, C Giraldo, H Hooghiemstra 2019 The flickering connectivity system of the north Andean páramos. Journal of Biogeography 46:1808–1825.

Folk RA, CM Siniscalchi, DE Soltis 2020 Angiosperms at the edge: Extremity, diversity, and phylogeny. Plant, Cell & Environment 43:2871–2893.

Friis EM, PR Crane, KR Pedersen 2011 Early Flowers and Angiosperm Evolution. Cambridge: Cambridge University Press.

Fritz SA, A Purvis 2010 Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. Conservation Biology 24:1042–1051.

Giulietti AM, JR Pirani, RM Harley 1997 Espinhaço range region Eastern Brazil. In: S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, & A. C. Hamilton (Eds), Centres of plant diversity. A guide and strategies for the conservation, Vol. 3. The Americas. WWF/IUCN:397–404.

Guindon S, O Gascuel 2003 A Simple, Fast, and Accurate Algorithm to Estimate Large Phylogenies by Maximum Likelihood. Systematic Biology 52:696–704.

Harris EM 1999 Capitula in the Asteridae: A widespread and varied phenomenon. The Botanical Review 65:348–369.

Hernández-Hernández T, JJ Wiens 2020 Why Are There So Many Flowering Plants? A Multiscale Analysis of Plant Diversification. The American Naturalist 195:948–963.

Hopper SD, H Lambers, FAO Silveira, PL Fiedler 2021 OCBIL theory examined: reassessing evolution, ecology and conservation in the world's ancient, climatically buffered and infertile landscapes. Biological Journal of the Linnean Society 133:266–296.

Hughes CE, RT Pennington, A Antonelli 2013 Neotropical Plant Evolution: Assembling the Big Picture. Botanical Journal of the Linnean Society 171:1–18.

Igea J, AJ Tanentzap 2020 Angiosperm speciation cools down in the tropics. Ecology Letters 23:692–700.

Inglis PW, TB Cavalcanti 2018 A molecular phylogeny of the genus diplusodon (Lythraceae), endemic to the campos rupestres and cerrados of South America. Taxon 67:66–82.

Landis MJ, NJ Matzke, BR Moore, JP Huelsenbeck 2013 Bayesian Analysis of Biogeography when the Number of Areas is Large. Systematic Biology 62:789–804.

Loeuille B, SC Keeley, JR Pirani 2015 Systematics and Evolution of Syncephaly in American Vernonieae (Asteraceae) with Emphasis on the Brazilian Subtribe Lychnophorinae. Systematic Botany 40:286–298.

Loeuille B, J Semir, LG Lohmann, JR Pirani 2015 A Phylogenetic Analysis of Lychnophorinae (Asteraceae: Vernonieae) Based on Molecular and Morphological Data. Systematic Botany 40:299–315.

Loeuille B, J Semir, JR Pirani 2019 A synopsis of Lychnophorinae (Asteraceae: Vernonieae). Phytotaxa 398:1–139.

Loeuille BFP 2011 Towards a phylogenetic classification of Lychnophorinae (Asteraceae: Vernonieae). São Paulo.

Louca S, M Doebeli 2018 Efficient comparative phylogenetics on large trees. Bioinformatics 34:1053–1055.

Lusa MG, BFP Loeuille, D Ciccarelli, B Appezzato-da-Glória 2018 Evolution of Stem and Leaf Structural Diversity: a Case Study in Lychnophorinae (Asteraceae). Botanical Review 84:203–241.

Maddison WP, PE Midford, SP Otto 2007 Estimating a Binary Character's Effect on Speciation and Extinction. Systematic Biology 56:701–710.

Main BY 1997 Granite outcrops: a collective ecosystem. Journal of the Royal Society of Western Australia 80:113–122.

Mandel JR, RB Dikow, CM Siniscalchi, R Thapa, LE Watson, VA Funk 2019 A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. Proceedings of the National Academy of Sciences 116:14083–14088.

Marques D, JB e Cândido, B Loeuille, J Marzinek 2022 Comparative morphology and anatomy of cypselae in Piptolepis (Vernonieae, Asteraceae) with emphasis on the pappus systematic significance. Flora 287:151988.

Mattos JS de, LPC Morellato, MGG Camargo, MA Batalha 2019 Plant phylogenetic diversity of tropical mountaintop rocky grasslands: local and regional constraints. Plant Ecology 220:1119–1129.

Matzke NJ 2014 Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Systematic Biology 63:951–970.

Maurin KJL 2020 Aug 16 An empirical guide for producing a dated phylogeny with treePL in a maximum likelihood framework.

May MR, S Höhna, BR Moore 2016 A Bayesian approach for detecting the impact of mass-extinction events on molecular phylogenies when rates of lineage diversification may vary. Methods in Ecology and Evolution 7:947–959.

Mucina L, GW Wardell-Johnson 2011 Landscape age and soil fertility, climatic stability, and fire regime predictability: Beyond the OCBIL framework. Plant and Soil 341:1–23.

Nevado B, N Contreras-Ortiz, C Hughes, DA Filatov 2018 Pleistocene glacial cycles drive isolation, gene flow and speciation in the high-elevation Andes. New Phytologist 219:779–793.

Oliveira RS, HC Galvão, MCR Campos, CB Eller, SJ Pearse, H Lambers 2015 Mineral nutrition of *campos rupestres* plant species on contrasting nutrient-impoverished soil types. New Phytologist 205:1183–1194.

Orme D 2018 The caper package: comparative analysis of phylogenetics and evolution in R.

Perez MF, IAS Bonatelli, EM Moraes, BC Carstens 2016 Model-based analysis supports interglacial refugia over long-dispersal events in the diversification of two South American cactus species. Heredity 116:550–557.

R Core Team 2020 A language and environment for statistical computing [Computer software].

Rabosky DL 2014 Automatic Detection of Key Innovations, Rate Shifts, and Diversity-Dependence on Phylogenetic Trees. PLoS ONE 9:e89543.

Ramírez-Barahona S, H Sauquet, S Magallón 2020 The delayed and geographically heterogeneous diversification of flowering plant families. Nature Ecology & Evolution 4:1232–1238.

Rapini A, C Bitencourt, F Luebert, D Cardoso 2021 An escape-to-radiate model for explaining the high plant diversity and endemism in campos rupestres†. Biological Journal of the Linnean Society 133:481–498.

Ree RH, BR Moore, CO Webb, MJ Donoghue 2005 A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 59:2299–2311.

Ree RH, SA Smith 2008 Maximum Likelihood Inference of Geographic Range Evolution by Dispersal, Local Extinction, and Cladogenesis. Systematic Biology 57:4–14.

Ribeiro PL, A Rapini, LS Damascena, C van den Berg 2014 Plant diversification in the Espinhaço Range: Insights from the biogeography of *Minaria* (Apocynaceae). Taxon 63:1253–1264.

Robinson HE 1999 Generic and subtribal classification of American Vernonieae. Smithsonian Contributions to Botany:1–116.

Ronquist F 1997 Dispersal-Vicariance Analysis: A New Approach to the Quantification of Historical Biogeography. Systematic Biology 46:195–203.

Schut AGT, GW Wardell-Johnson, CJ Yates, G Keppel, I Baran, SE Franklin, SD Hopper, KP van Niel, L Mucina, M Byrne 2014 Rapid Characterisation of Vegetation Structure to Predict Refugia and Climate Change Impacts across a Global Biodiversity Hotspot. PLoS ONE 9:e82778.

Silveira FAO, M Barbosa, W Beiroz, M Callisto, DR Macedo, LPC Morellato, FS Neves, YRF Nunes, RR Solar, GW Fernandes 2019 Tropical mountains as natural laboratories to study global changes: A long-term ecological research project in a megadiverse biodiversity hotspot. Perspectives in Plant Ecology, Evolution and Systematics 38:64–73.

Silveira FAO, PL Fiedler, SD Hopper 2021 OCBIL theory: a new science for old ecosystems. Biological Journal of the Linnean Society 133:251–265.

Silveira FAO, D Negreiros, NPU Barbosa, E Buisson, FF Carmo, DW Carstensen, AA Conceição, TG Cornelissen, L Echternacht, GW Fernandes, et al. 2016 Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant and Soil 403:129–152.

Simon MF, R Grether, LP de Queiroz, C Skema, RT Pennington, CE Hughes 2009 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences 106:20359–20364.

Simon MF, T Pennington 2012 Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. International Journal of Plant Sciences 173:711–723.

Smith SA, BC O'Meara 2012 TreePL: Divergence time estimation using penalized likelihood for large phylogenies. Bioinformatics 28:2689–2690.

Stamatakis A 2014 RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.

Stebbins GL 1967 Adaptive radiation and trends of evolution in higher plants. In: Dobzhansky T, Hecht MK, Steere WC, editors. Evolutionary biology. Vol. 1. New York: Appleton-Century-Crofts. p. 101–142.

Stuessy TF, D Garver 1996 The defensive role of pappus in heads of Compositae. In: Caligari PDS, Hind DJN, editors. Compositae: biology and utilization. Proceedings of the International Compositae Conference. London: Royal Botanic Garden, Kew. p. 81–91.

Vamosi JC, SM Vamosi 2011 Factors influencing diversification in angiosperms: At the crossroads of intrinsic and extrinsic traits. American Journal of Botany 98:460–471.

Vasconcelos TNC, S Alcantara, CO Andrino, F Forest, M Reginato, MF Simon, JR Pirani 2020 Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. Proceedings of the Royal Society B: Biological Sciences 287.

Wiens JJ, CH Graham 2005 Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Zappi DC, MF Moro, TR Meagher, EN Lughadha 2017 Plant Biodiversity Drivers in Brazilian Campos Rupestres: Insights from Phylogenetic Structure. Frontiers in Plant Science 8.

Figures legends

Figure 1. Lychnophorinae phylogenetic dated tree. Blue bars are the node ages confidence intervals; red numbers are the bootstrap support; under the tree is the geological time stratigraphy.

Figure 2. Leaf sheath character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure 3. Pappus series character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure 4. Pappus type character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure 5. Pappus duration character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure 6. The BAYAREALIKE+J+X biogeographical model. The node letters represent the ancestral range estimated areas and tip letters the actual species distribution areas. A = Chapada Diamantina; B = Espinhaço Septentrional; C = Espinhaço Meridional; D = Brasília Arc; E = Restinga; F = Caatinga; G = Cerrado; H = Ceará.

Figure 7. The mirror cladogram comparing the results of the Ancestral State Reconstruction (ASR) for syncephaly and number of florets in capitula. Nodes graphs represents the likelihoods of the ancestral states. Branches are coloured according to the most probable state in each node.

Figure A1. Habit character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure A2. Bladder-like trichome character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure A3. Syncephaly character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure A4. Florets per capitulum character states estimated in Lychnophorinae phylogeny as a result of the Ancestral State Reconstruction (ASR) analysis using the Markov model of evolution with an ARD (all rates can be different) rate model. The character states likelihoods are expressed in the colours proportions.

Figure A5. The BAYAREALIKE+J+X biogeographical model with the node pies indicating the proportion of each ancestral range estimated area in the respective node.

Figure A6. Areas used to reconstruct the biogeographic history of Lychnophorinae through BioGeoBEARS, based on the biogeographic patterns presented by Alves and Loeuille (2021).

Figure A7. Histograms showing the counts of different events that was calculated in the Biogeographical Stochastic Mapping (BSM) of the BAYAREALIKE+J+X model. The number of events is displayed in the x-axis and the corresponding stochastic map number are displayed in the y-axis.

Figure A8. Comparison between the ancestral range probabilities at each internal node (displayed in the x-axis) and the mean of 1000 stochastic maps at each internal node (displayed in the y-axis), both from the BAYAREALIKE+J+X model. The 95% confidence intervals are indicated by the vertical lines.

Table 1. The D values of the phylogenetic signal analysis for each morphological character state their respective brownian evolution model significance (P Brownian) and random evolution model significance (P Random).

Character state	D value	P Brownian	P Random
Pappus Paleaceous	-0.0824	0.6127	0
Pappus Setose	-0.1870	0.7206	0
Pappus Caducous	0.3121	0.1796	2.00^{-04}
Pappus Persistent	0.2148	0.2806	0
Pappus Uniseriate	0.2201	0.3651	0.0159
Pappus Biseriate	0.2006	0.2758	0
Pappus Multiseriate	-0.2014	0.7114	0
1 Floret	0.1782	0.3588	0
2-9 Florets	0.3801	0.0744	2.00^{-04}
10-60 Florets	-0.0134	0.5293	0
100 Florets	0.6905	0.3784	0.2726
Habit Candelabriform	-0.8449	0.9983	0
Habit Caulirosula	-0.7232	0.9311	0
Habit Shrub	-0.4600	0.8665	0
Habit Treelet	-0.4892	0.9592	0
Sheath Absence	-0.7735	0.9973	0
Sheath Amplexical	-0.7481	0.9974	0
Sheath Pad-like	-0.8219	0.9602	0
Syncephalia	0.1850	0.2462	0
Bladder-like Trichome	-0.1554	0.7186	0

Table 2. Ancestral State Reconstruction (ASR) summary showing the loglikelihoods and Akaike Information Criterion (AIC) values calculated for each morphological character and reconstruction model. ER = equal rates model; SYM = transition rate i–>j is equal to transition rate j–>i model; SUEDE = only stepwise transitions i–>i+1 and i–>i-1 allowed, all ‘up’ transitions are equal, all ‘down’ transitions are equal model; SRD = only stepwise transitions i–>i+1 and i–>i-1 allowed and each rate can be different model; ARD = all rates can be different.

Character	loglikelihood ARD	AIC ARD	loglikelihood ER	AIC ER	loglikelihood SRD	AIC SRD	loglikelihood SUEDE	AIC SUEDE	loglikelihood SYM	AIC SYM
Habit	-43.94695	111.8939	-47.49491	118.9898	-47.91649	119.833	-50.82173	125.64346	-45.06115	114.1223
Bladder-like trichome	-39.95584	83.91168	-42.59929	89.19858	-39.95584	83.91168	-39.95584	83.91168	-42.59929	89.19858
Sheath	-25.1649	62.3298	-29.66076	71.32152	-29.39226	70.78452	-29.73256	71.46512	-29.06494	70.12988
Syncephalia	-43.06159	90.12318	-43.3471	90.6942	-43.06159	90.12318	-43.06159	90.12318	-43.3471	90.6942
Florets	-64.49902	152.998	-84.36357	192.7271	-67.94531	159.8906	-78.49151	180.98302	-73.68021	171.3604
Pappus	-38.40645	88.8129	-48.44238	108.8848	-46.19946	104.3989	-50.85711	113.71422	-47.21327	106.4265
Pappus type	-30.63748	65.27496	-30.68108	65.36216	-30.63748	65.27496	-30.63748	65.27496	-30.68108	65.36216
Pappus duration	-36.41817	76.83634	-37.19347	78.38694	-36.41817	76.83634	-36.41817	76.83634	-37.19347	78.38694

Table 3. Summary of the biogeographical models results. Models = model used name; LnL = log likelihood; Nº parameters = number of parameters used for the respective model; d = dispersal; e = extinction; j = jump dispersal; x = dispersal probability as a function of distance; AIC = Akaike Information Criterion; AIC_wt = Akaike Information Criterion weight.

Models	LnL	Nº parameters	d	e	j	x	AIC	AIC_wt
DEC	-242.2	2	0.11	0.091	0	0	488.4	2.2^{-14}
DEC+X	-233.8	3	4.34	0.28	0	-0.52	473.5	3.6^{-11}
DEC+J	-239.0	3	0.099	0.043	0.0091	0	484.1	1.8^{-13}
DEC+J+X	-233.3	4	0.53	0.060	0.055	-0.28	474.5	2.2^{-11}
DIVALIKE	-254.3	2	0.13	0.10	0	0	512.5	1.2^{-19}
DIVALIKE+X	-240.2	3	4.99	0.072	0	-0.56	486.4	5.7^{-14}
DIVALIKE+J	-248.3	3	0.10	1.0^{-12}	0.013	0	502.5	1.8^{-17}
DIVALIKE+J+X	-254.1	4	0.13	0.10	0.0001	0	516.2	1.9^{-20}
BAYAREALIKE	-235.1	2	0.10	0.63	0	0	474.2	2.5^{-11}
BAYAREALIKE+X	-230.8	3	1.18	0.61	0	-0.37	467.5	7.2^{-10}
BAYAREALIKE+J	-217.1	3	0.060	0.24	0.014	0	440.1	0.0006
BAYAREALIKE+J+X	-208.7	4	2.78	0.19	0.43	-0.58	425.4	1.00

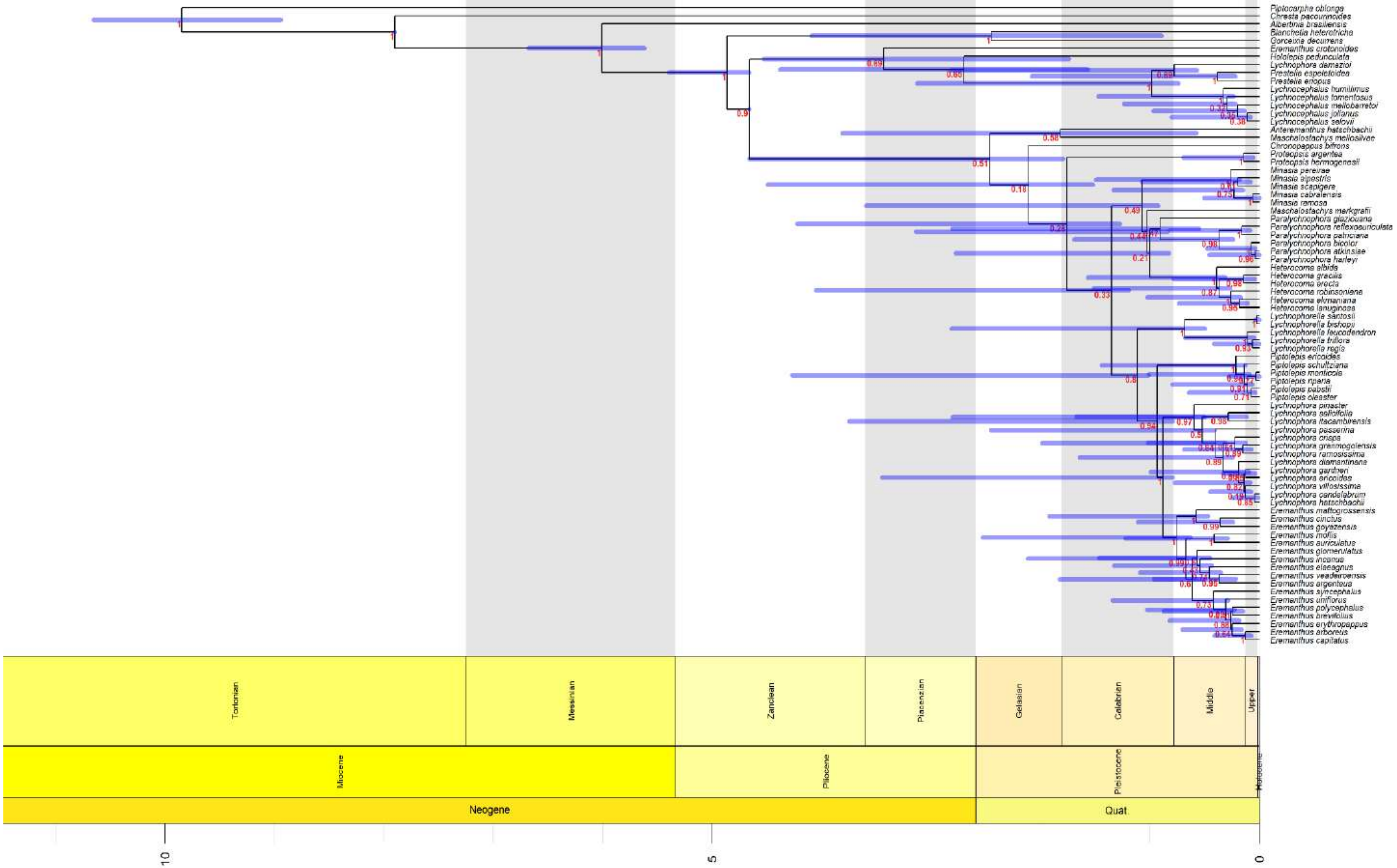
Table 4. Summary of the Biogeographical Stochastic Mapping. j = founder/jump dispersal events; a = anagenetic event; d = dispersal event; e = extinction event; s = subset sympatry events; v = vicariance events; y = sympatry events; ALL_disp = anagenetic plus cladogenetic dispersals events; ana_disp = anagenetic dispersal events; all_ana = all anagenetic dispersal events; all_clado = all cladogenetic events; total_events = event summation.

	j	a	d	e	s	v	y	ALL_disp	ana_disp	all_ana	all_clado	total_events
means	12.92	0	0	0	0	0	63.08	12.92	0	0	76	76
stdevs	1.53	0	0	0	0	0	1.530	1.530	0	0	0	0
sums	12917	0	0	0	0	0	63083	12917	0	0	76000	76000

Table 5. Counts of founder dispersal events estimated by Biogeographical Stochastic Mapping. The first column is the dispersal origin area and the first row is the dispersal target area.

Areas	Chapada Diamantina (A)	Espinhaço Septentrional (B)	Espinhaço Meridional (C)	Brasília Arc (D)	Restinga (E)	Caatinga (F)	cerrado (G)	Ceará (H)
Chapada Diamantina (A)	0	0.082	0.140	0.170	0.003	0.031	0.007	0.150
Espinhaço Septentrional (B)	1.790	0	0.260	0.670	0.010	0.022	0.066	0.150
Espinhaço Meridional (C)	2.180	0.270	0	3.390	0.051	0.015	0.071	0.019
Brasília Arc (D)	0.180	0.270	1.510	0	0.029	0.005	0.018	0.250
Restinga (E)	0.009	0.026	0.380	0.013	0	0.004	0	0.210
Caatinga (F)	0.008	0.016	0.067	0.007	0.001	0	0.002	0.230
Cerrado (G)	0.006	0.006	0.038	0.019	0.003	0.004	0	0.002
Ceará (H)	0.002	0.010	0.023	0.002	0.002	0.002	0	0

Figure 1.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Prestelia eriopus
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Lychnocephalus jolianus
Lychnocephalus sellowii
Anteremanthus hatschbachii
Maschalostachys mellosilvae
Chronopappus bifrons
Proteopsis argentea
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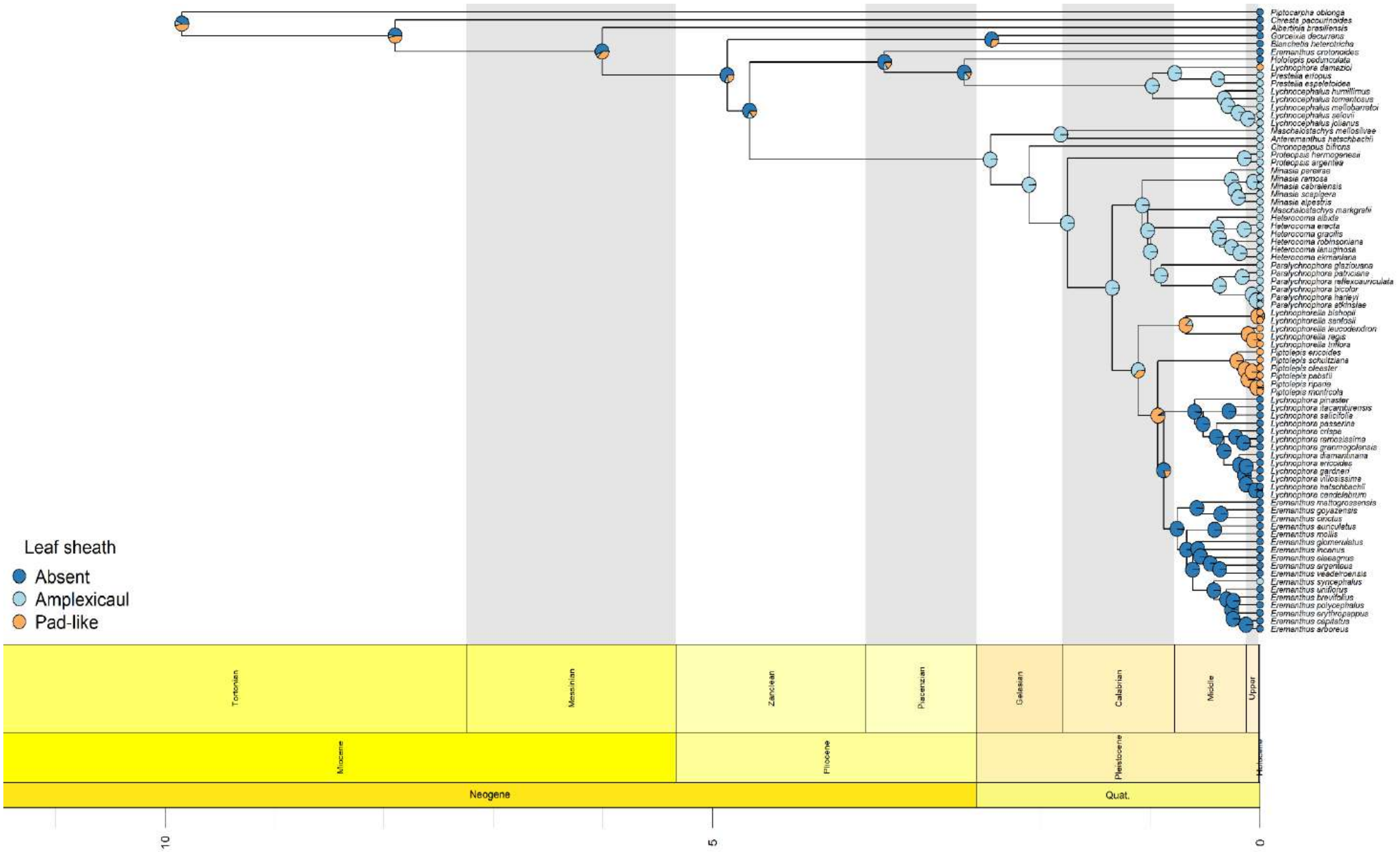
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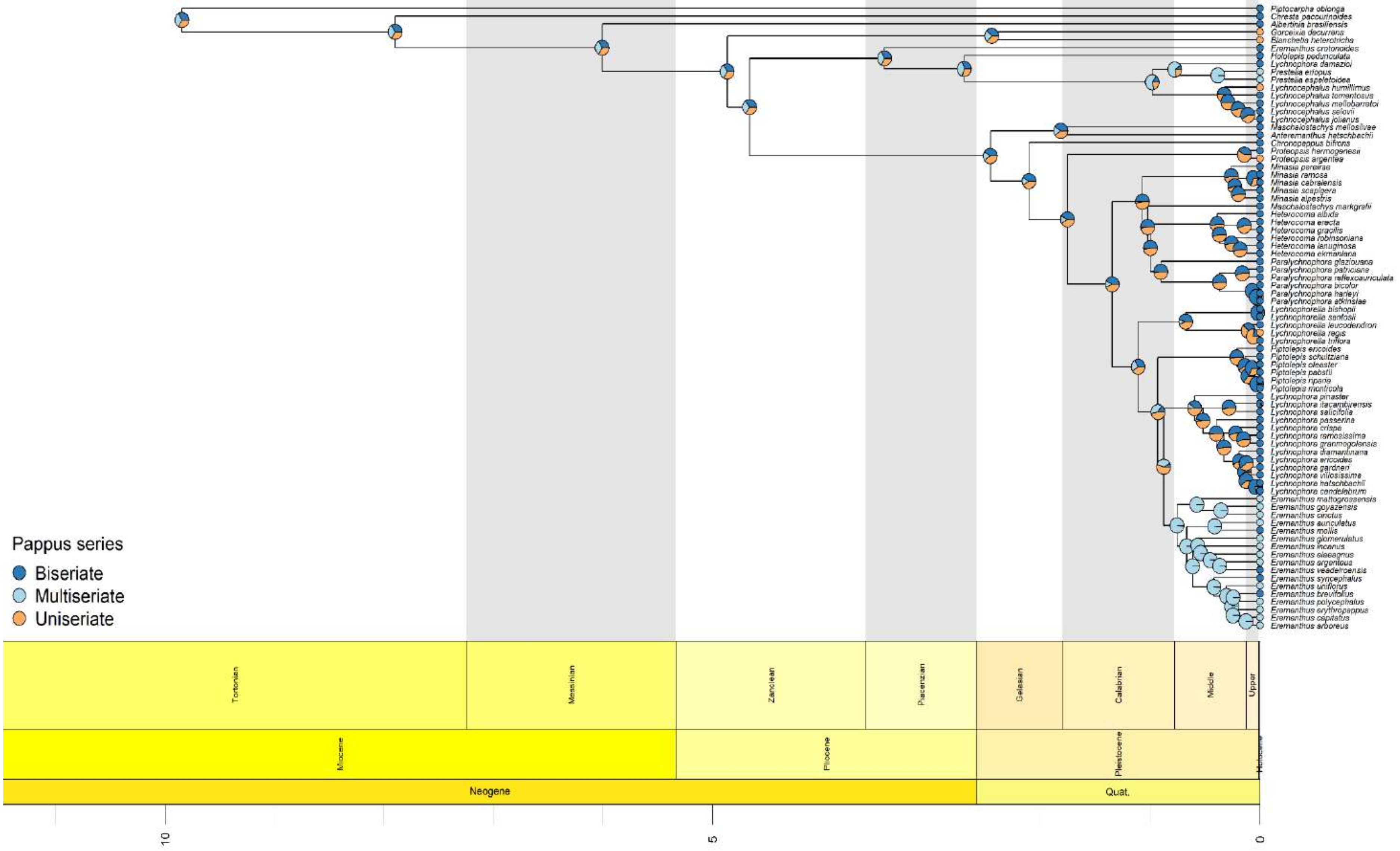
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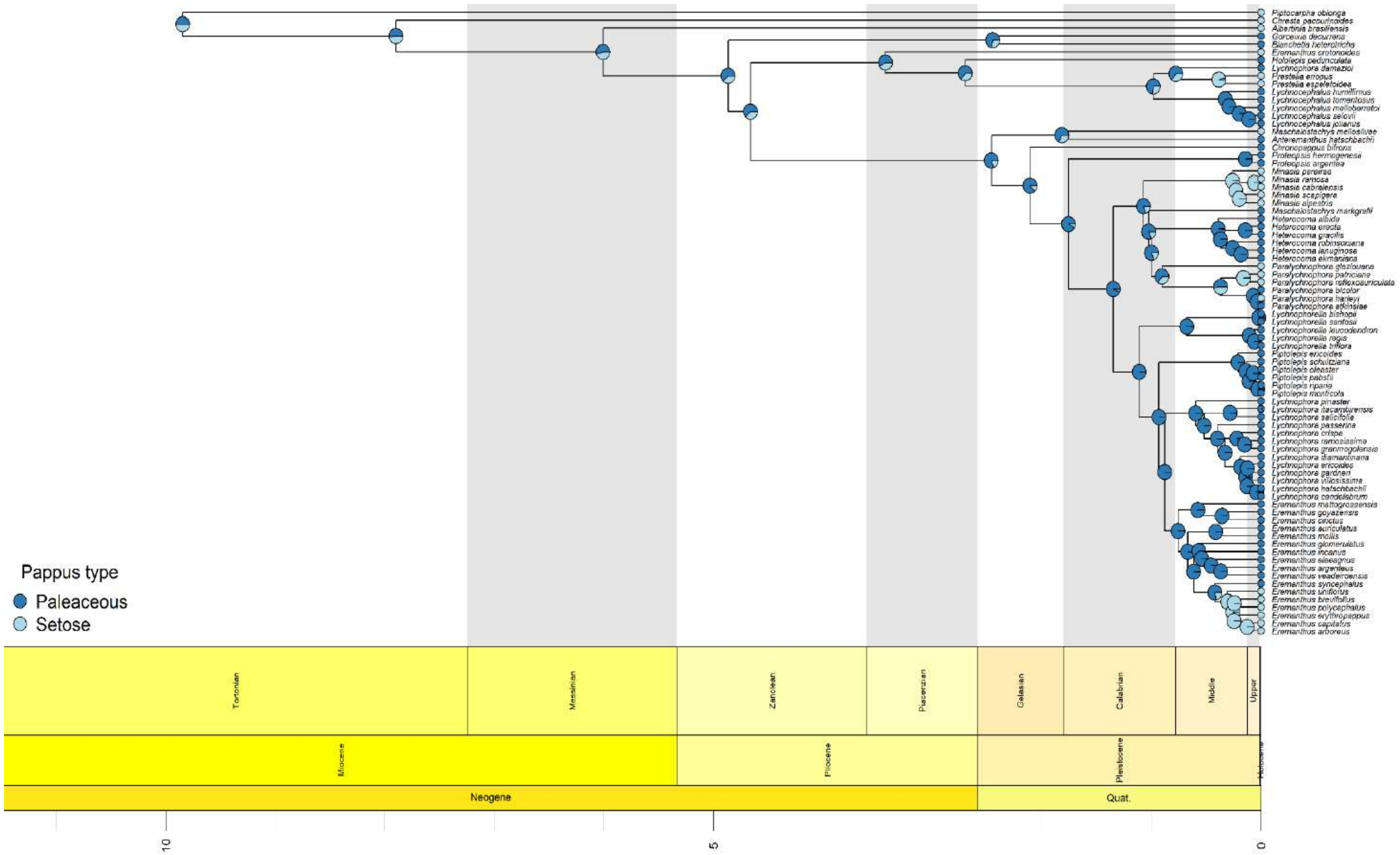
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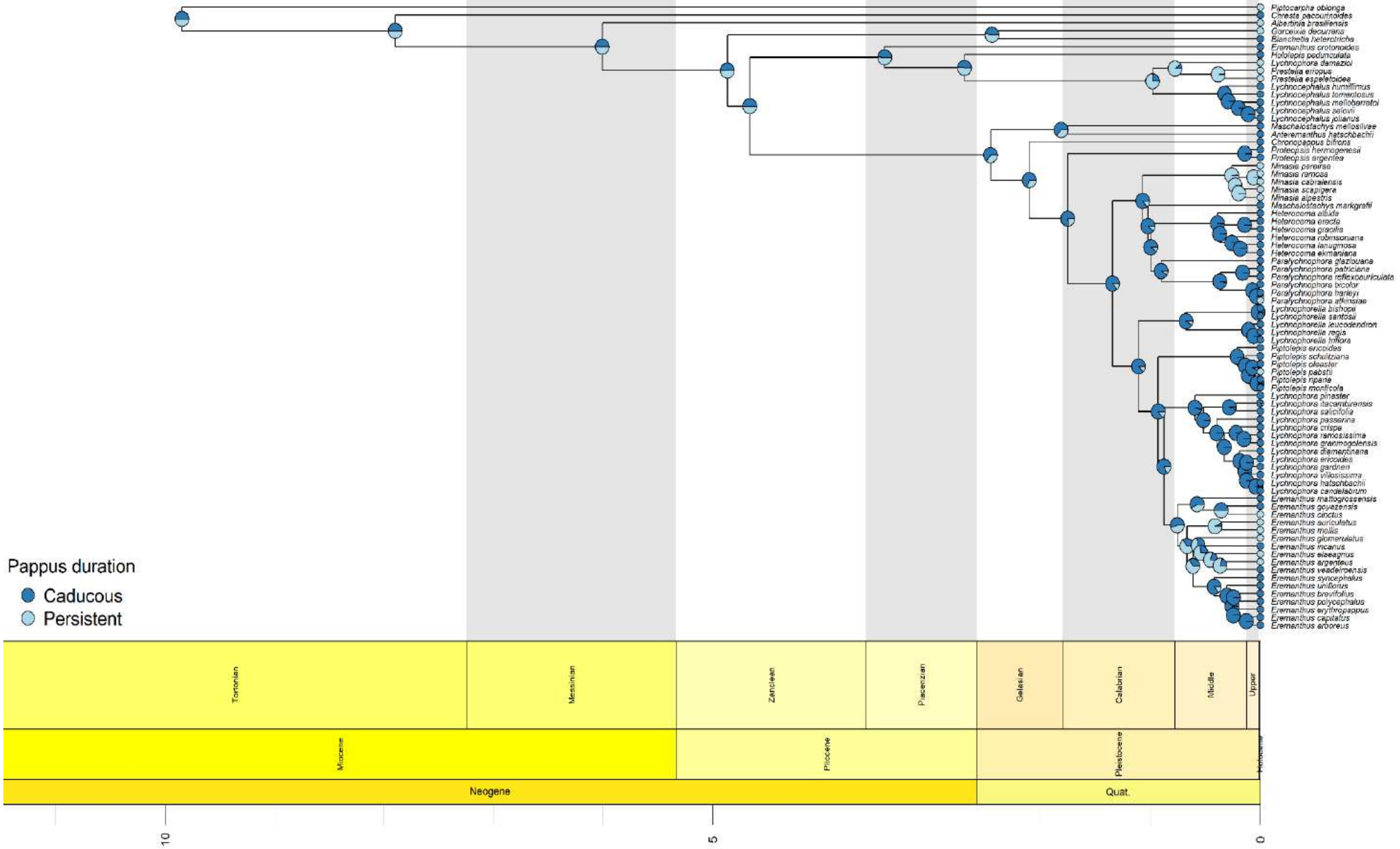
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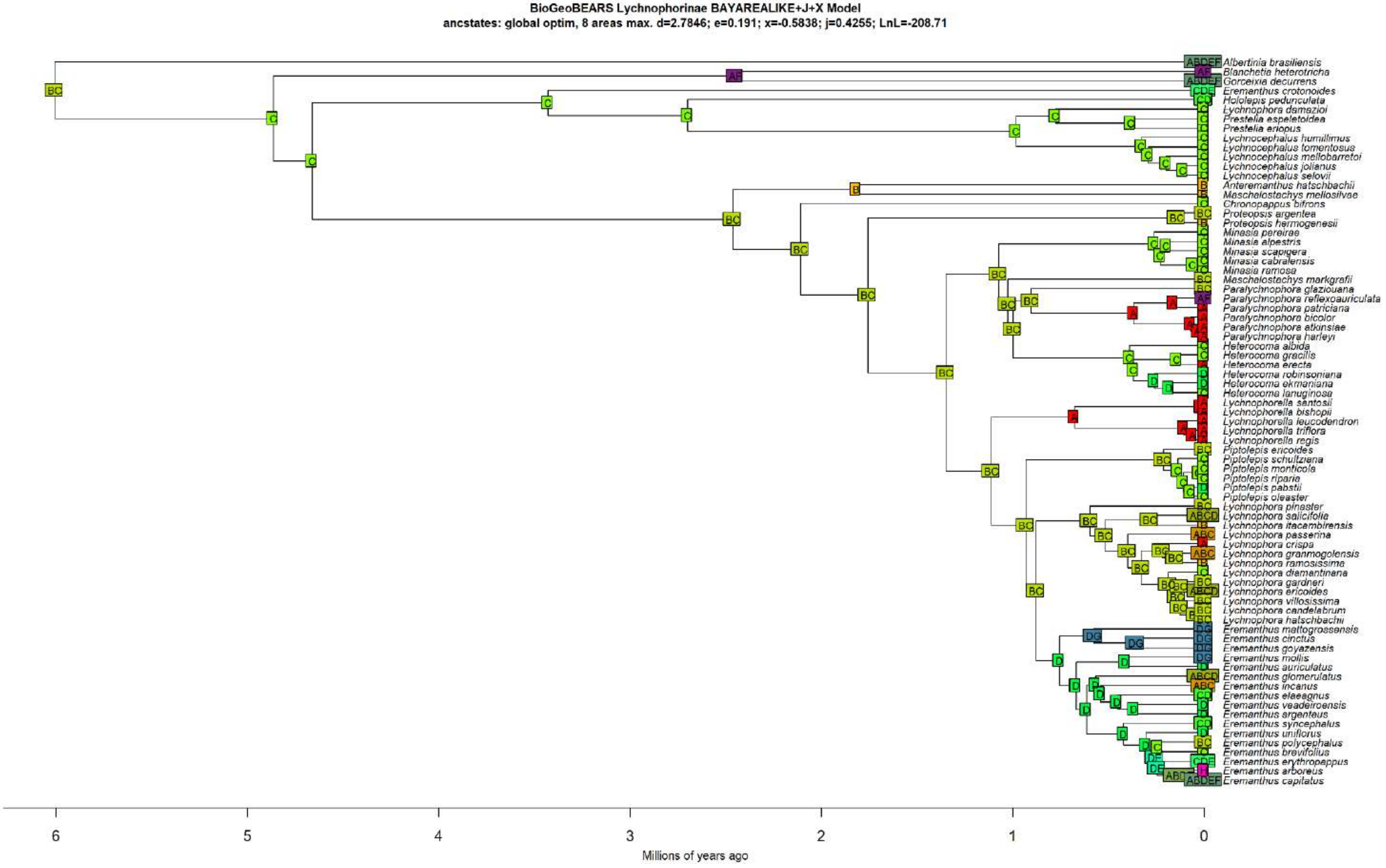
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Chronopappus bifrons
Proteopsis argentea
Proteopsis hermogenesii
Minasia pereirae
Minasia alpestris
Minasia scapigera
Minasia cabralensis
Minasia ramosa
Maschalostachys markgrafii
Paralychnophora glaziouana
Paralychnophora reflexoauriculata
Paralychnophora patriciana
Paralychnophora bicolor
Paralychnophora atkinsiae
Paralychnophora harleyi
Heterocoma albida
Heterocoma gracilis
Heterocoma erecta
Heterocoma robinsoniana
Heterocoma ekmaniana
Heterocoma lanuginosa
Lychnophorella santosii
Lychnophorella bishopii
Lychnophorella leucodendron
Lychnophorella triflora
Lychnophorella regis
Piptolepis ericoides
Piptolepis schultziana
Piptolepis monticola
Piptolepis riparia
Piptolepis pabstii
Piptolepis oleaster
Lychnophora pinaster
Lychnophora salicifolia
Lychnophora itacambirensis
Lychnophora passerina
Lychnophora crispa
Lychnophora granmogolensis
Lychnophora ramosissima
Lychnophora diamantinana
Lychnophora gardneri
Lychnophora ericoides
Lychnophora villosissima
Lychnophora candelabrum
Lychnophora hatschbachii
Eremanthus mattogrossensis
Eremanthus cinctus
Eremanthus goyazensis
Eremanthus mollis
Eremanthus auriculatus
Eremanthus glomerulatus
Eremanthus incanus
Eremanthus elaeagnus
Eremanthus veadeiroensis
Eremanthus argenteus
Eremanthus syncephalus
Eremanthus uniflorus
Eremanthus polycephalus
Eremanthus brevifolius
Eremanthus erythropappus
Eremanthus arboreus
Eremanthus capitatus
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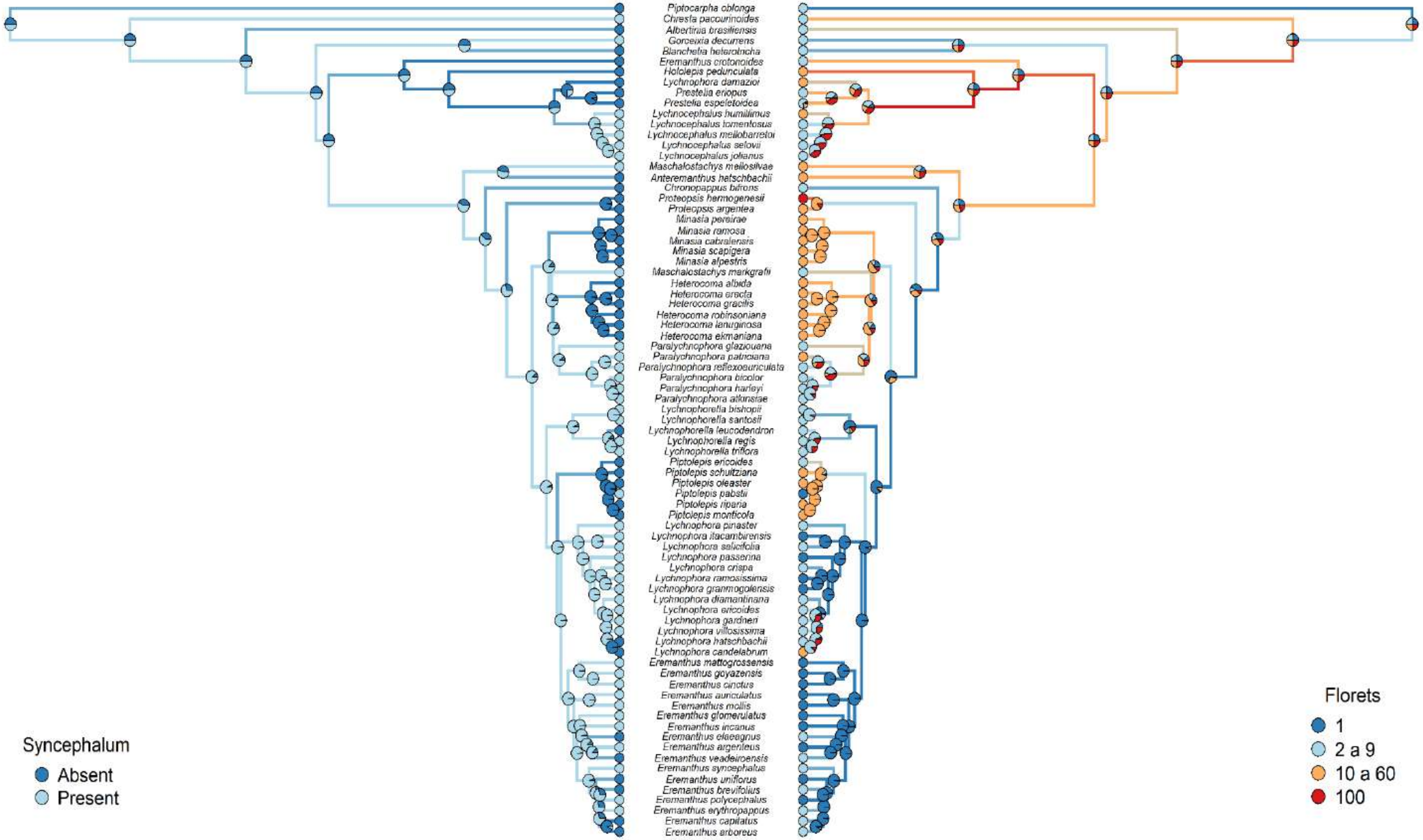
5
4
3
2
1
0
Millions of years ago

Figure 7.


Piptocarpha oblonga
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Albertinia brasiliensis
Gorceixia decurrens
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Eremanthus crotonoides
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Lychnophora damazioi
Prestelia eriopus
Prestelia espeletoidea
Lychnocephalus humillimus
Lychnocephalus tomentosus
Lychnocephalus mellobarretoi
Lychnocephalus sellowii
Lychnocephalus jolianus
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Eremanthus incanus
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Eremanthus argenteus
Eremanthus veadeiroensis
Eremanthus syncephalus
Eremanthus uniflorus
Eremanthus brevifolius
Eremanthus polycephalus
Eremanthus erythropappus
Eremanthus capitatus
Eremanthus arboreus
Syncephalum
Absent
Present
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1
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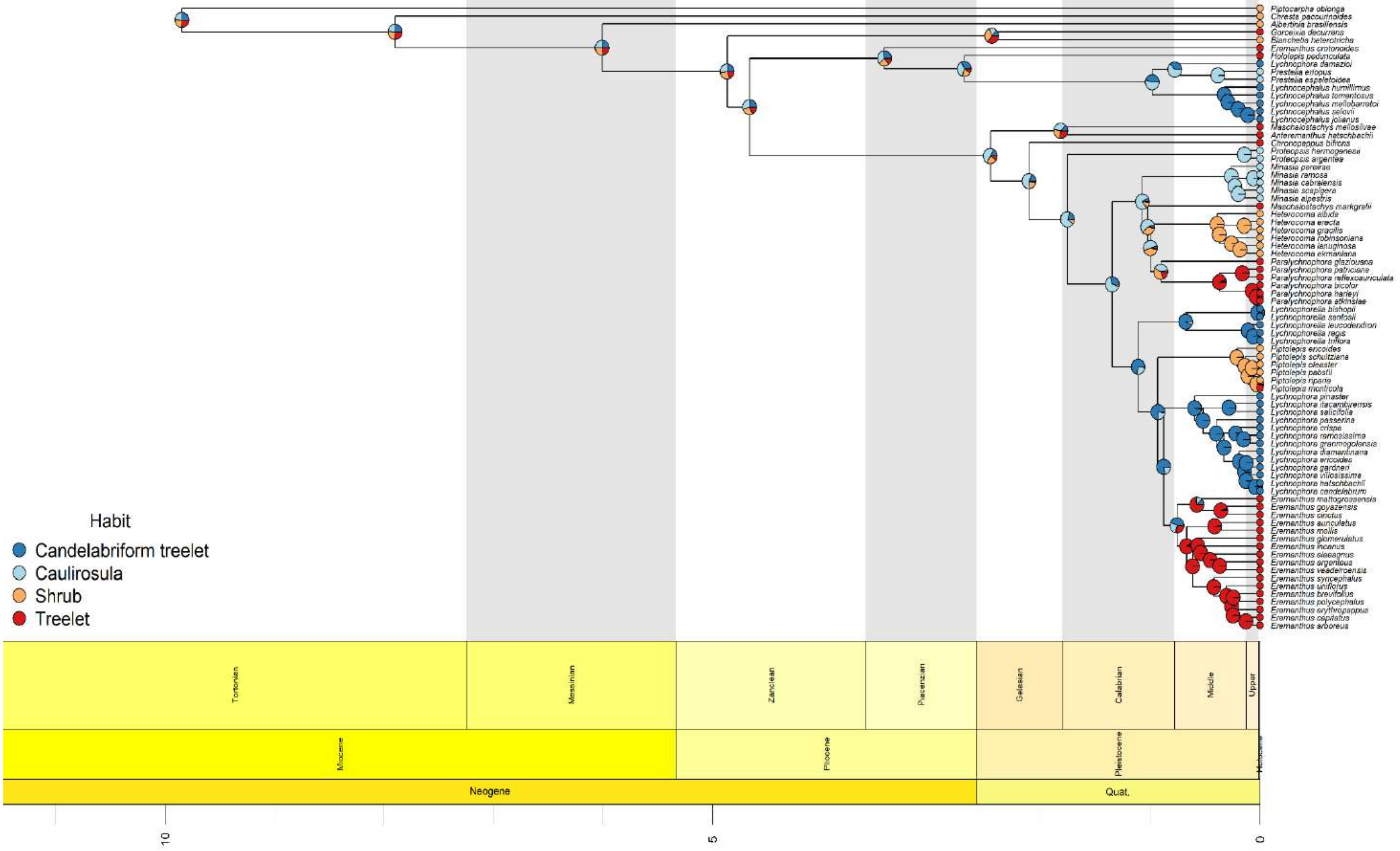
Supplementary figure A1



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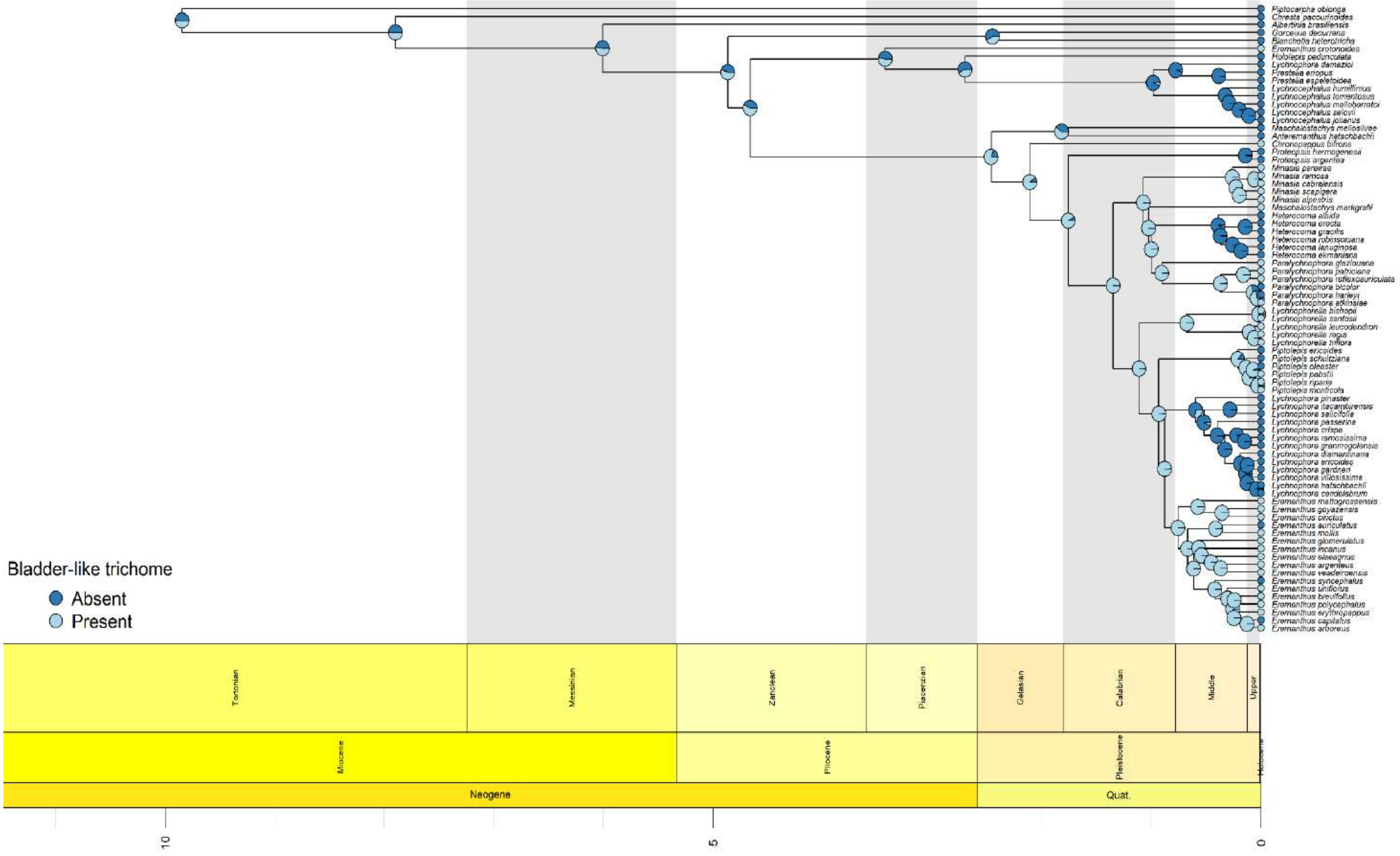

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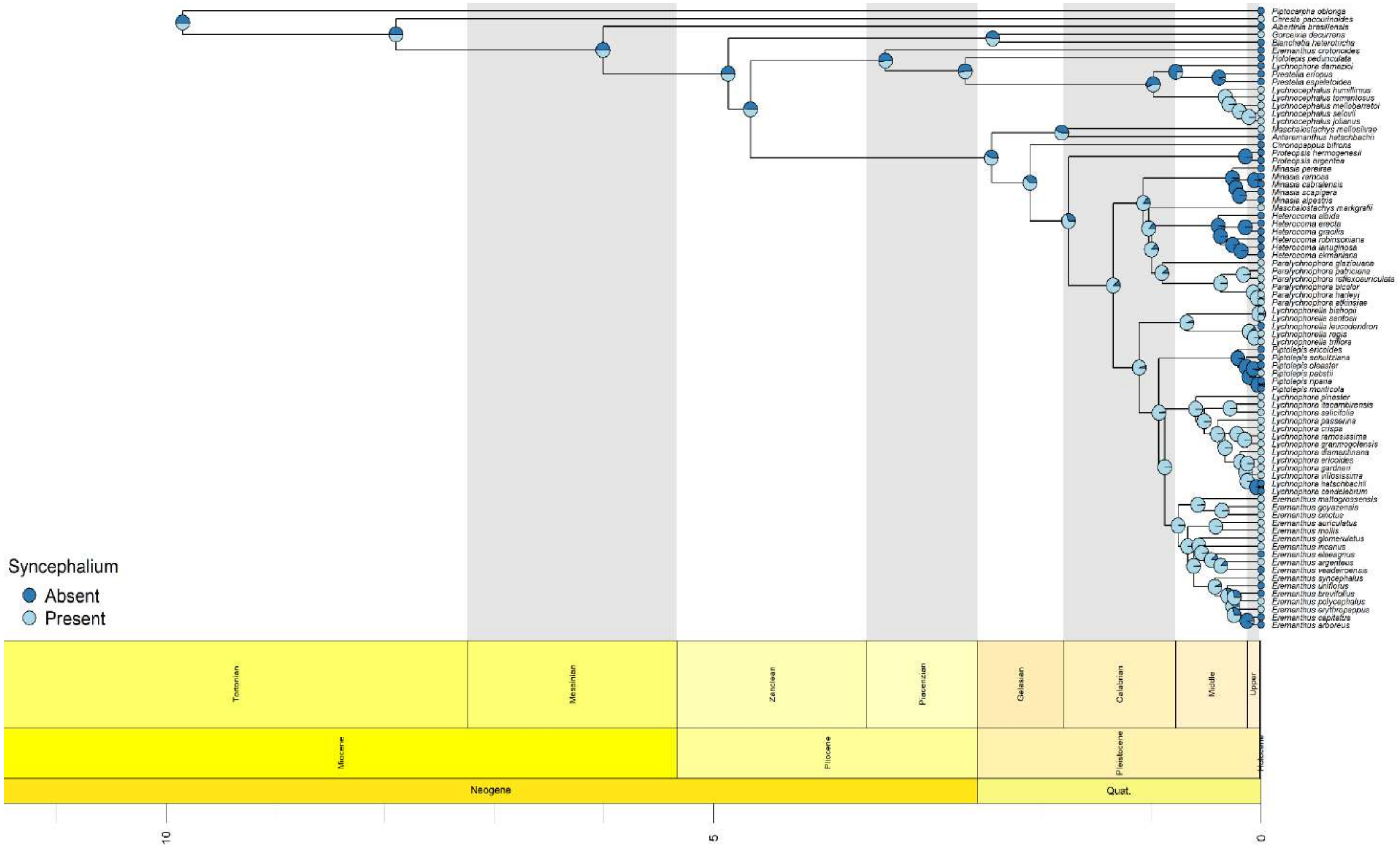

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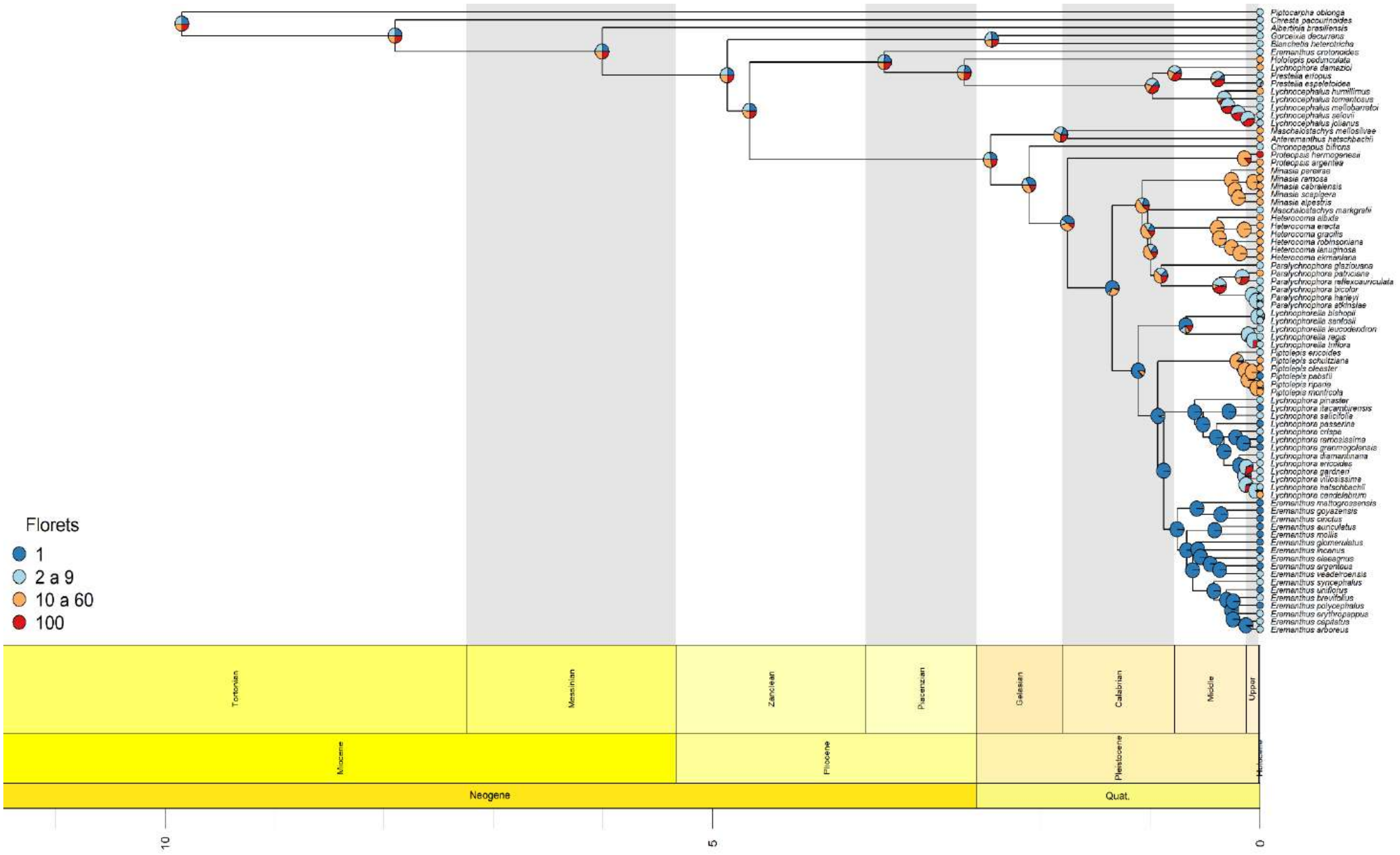
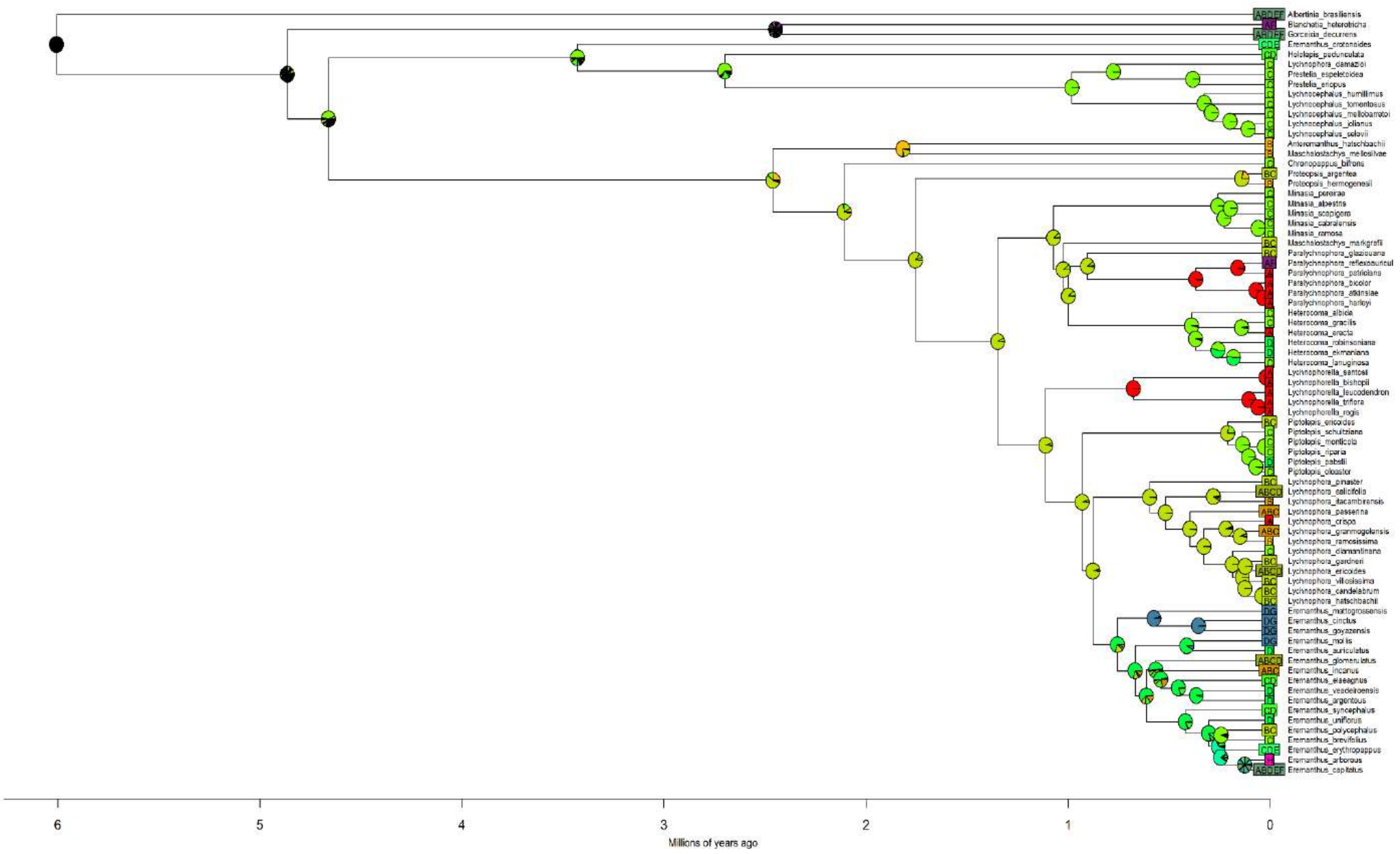


Supplementary figure A5

BioGeoBEARS Lychnophorinae BAYAREALIKE+J+X Model
ancstates: global optim, 8 areas max. d=2.7846; e=0.191; x=-0.5838; j=0.4255; LnL=-208.71



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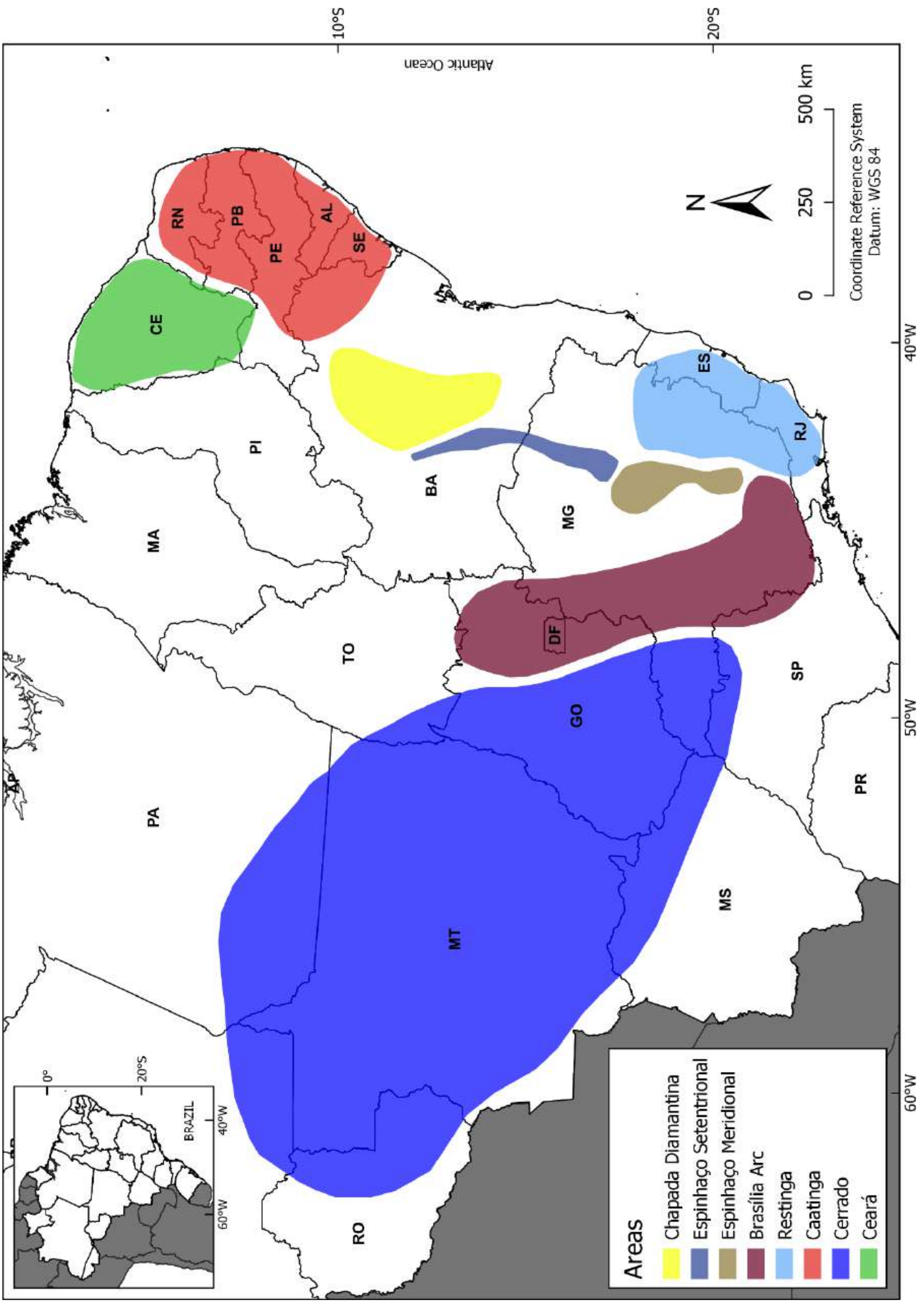

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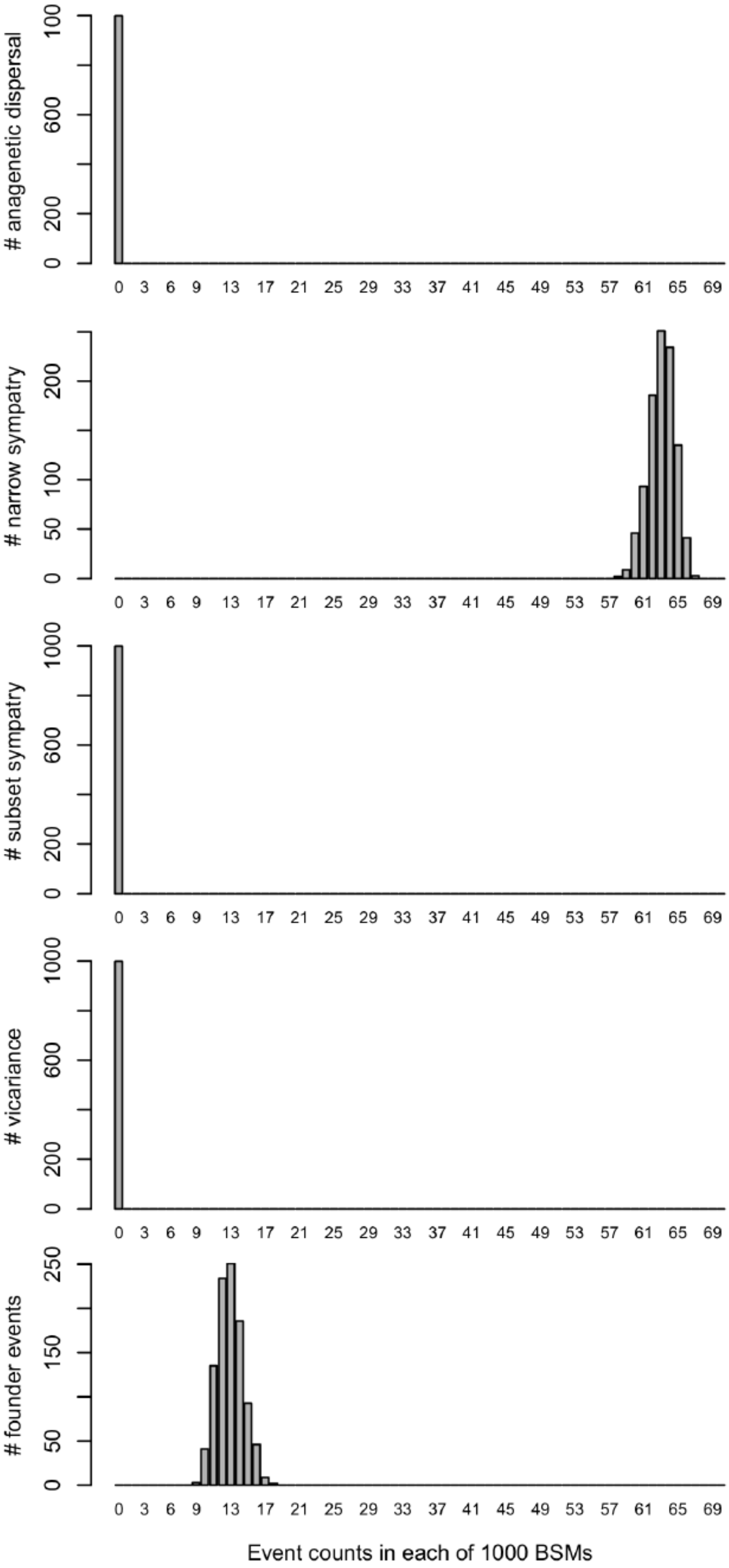

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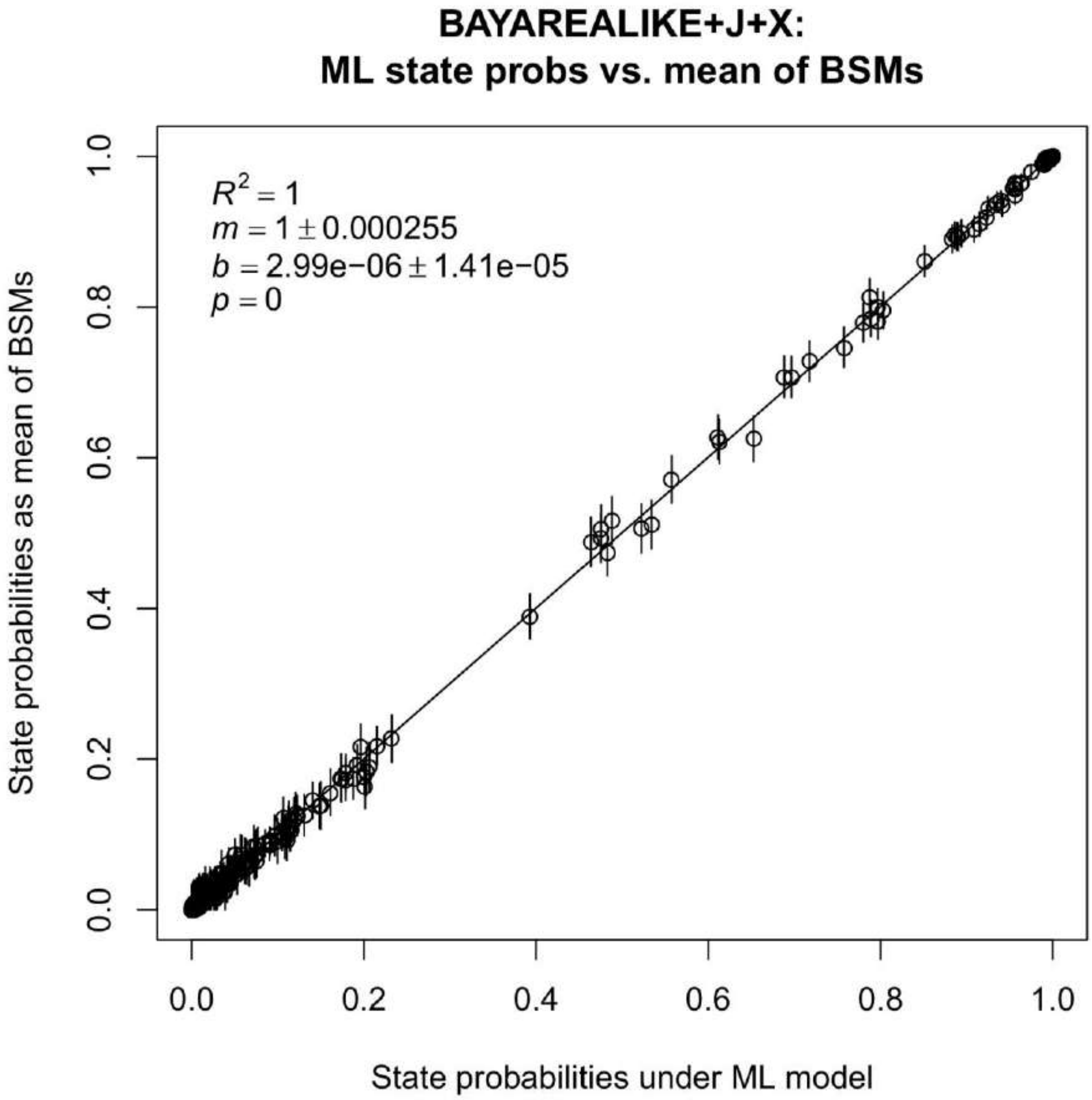

4 ARTIGO 2 – THE FUTURE SCENARIO OF AN ICONIC TREE FROM THE BRAZILIAN CERRADO: PERSPECTIVES ON *EREMANTHUS* LESS. (ASTERACEAE) CONSERVATION[1]

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Abstract

Characterized as one of the largest biodiversity hotspots, the Cerrado ecoregion houses a wide variety of endemic species. Several threats, such as agricultural expansion and habitat fragmentation, put the species of the Cerrado ecosystems and biodiversity at risk. The genus *Eremanthus* is frequent in the Cerrado and suffers from intense anthropogenic pressure due to overexploitation mainly for the construction of fences and extraction of essential oil. Environmental suitability, of the Mid-Holocene, present and future (2070), were estimated for the genus in order to characterize the importance of the climate in the species distribution and to analyse the conservation status. The Species Distribution Modelling showed that most species of *Eremanthus* presented similarities between the environmental suitability of the present and the Mid-Holocene, enabling the identification of areas of environmental stability in OSL areas of campos rupestres. The species of the genus were classified as Endangered and Vulnerable according to IUCN criteria, presenting very reduced areas of environmental suitability projected in the future and a low percentage of species in Protected Areas, that may influence possible extinctions of species in the genus. The approaches in this study provide consistent subsidies to assist in conservation planning.

Keywords: Campos rupestres, Environmental suitability, Espinhaço Range, Occupancy, Occurrence, Threatened species

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[1] A ser submetido ao periódico Plant Systematics and Evolution

Introduction

The Cerrado, occupying the central portion of Brazil, part of Bolivia and Paraguay, is the largest neotropical savannah, whose biogeographical and morpho-climatic domain extends over about 2 million km^2. It is widely recognized as one of the largest biodiversity hotspots in the world due to its high species richness and index of endemism, with 44% of the total plant species and 80% of its woody plants exclusive to this environment (Lenthall et al. 1999; Klink and Machado 2005). The high environmental heterogeneity of the Cerrado favours the floristic diversity of plant communities, especially through the variety of soils (latosols, cambisols, gleis, hydromorphic laterite, litholic, sands quartzous, podzolic oxisols), climates and geomorphologies (Siqueira and Durigan 2007; Souza-Neto et al. 2016).

The dynamics of vegetation in the Cerrado is strongly influenced by wildfires, promoting the maintenance of various phytophysiognomies, with plants having different fire-resistance adaptations and fire dependence in their reproduction cycle (Simon et al. 2009; Simon and Pennington 2012; Rissi et al. 2017; Loram-Lourenço et al. 2020). The species richness in the Cerrado originates from the recent diversification of some endemic genera that occurred at approximately 10 Mya, coinciding with the expansion of C4 grasses during the Miocene (Simon et al. 2009).

The campos rupestres constituted one of the Cerrado physiognomies in this ecoregion, but recently it was recognized as a different and independent ecoregion and in this study Cerrado and campos rupestres will be treated as distinct phytophysiognomies, in agreement with recent ecoregion proposals (Colli-Silva et al. 2019; Morrone et al. 2022). Campos rupestres present remarkable topographic features with the presence of rock outcrops, promoting an endemic habitat for several species (Alves et al. 2014).

Despite the great importance of its biodiversity, the Cerrado suffers from intense environmental degradation. Currently, less than 20% of the Cerrado native vegetation is protected within reserves, with an estimated loss of 46% of its native vegetation; land use projections foresee intense deforestation in the coming decades (Strassburg et al. 2017; Terra et al. 2017). Environmental protection areas correspond to 6.5% of the Cerrado and only 3% of the natural vegetation is included in strictly protected areas in IUCN categories I to III (Françoso et al. 2015). There is an urgent need to preserve the Cerrado and campos rupestres biodiversity and scientific research towards this goal has in the last two decades contributing to the identification of biogeographic districts, assessment of land use and protected areas, spatial-temporal analysis of deforestation, climate studies, effects of fire on biodiversity dynamics, survey of threats and proposals to control them (Guisan et al. 2013; Françoso et al. 2015; Velazco et al. 2019; Colli et al. 2020; Fernandes et al. 2020).

The main threats to the Cerrado biodiversity are uncontrolled agricultural expansion that causes deforestation, habitat fragmentation and pollution of waterbodies with fertilizers and lime, intentional burning and replacement of Cerrado vegetation by exotic grasses to establish cattle pastures, which interfere in the natural ecosystem cycle (Klink and Machado 2005; Scarano et al. 2014) (Fig. 1). The campos rupestres are also under several and constant threats to biodiversity, such as mining, cattle overgrazing, invasion by exotic species, urban growth and native species overexploitation (Pena et al. 2017; Fernandes et al. 2020).

The OSL theory presents hypotheses regarding ecology, evolution and biological conservation in Old Stable Landscapes (OSL), which help to better understand areas that need greater biodiversity conservation (Mucina and Wardell-Johnson 2011). OSLs are landscapes that remained stable for millions of years and are characterized mainly by climatic stability and impoverished soils, all contributing to increased persistence of species lineages, maintenance of diversity and endemism, favouring the variability of fragmented population systems (Hopper 2009; Hopper et al. 2021; Silveira et al. 2021). The OSLs states that species in these environments tend to have limited seed dispersibility, which increases genetic divergence and allopatric speciation, high environmental specialization and phylogenetic niche conservatism (Hopper 2009; Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Fiorini et al. 2019).

The Cerrado and campos rupestres harbour many endemic species of *Eremanthus* (Asteraceae, Vernonieae) and both phytophysiognomies are considered an important biodiversity hotspot, but the latter is also considered an important OSL area (Mucina and Wardell-Johnson 2011; Silveira et al. 2016, 2020; Loeuille et al. 2019; Hopper et al. 2021). *Eremanthus* is a neotropical genus of treelets or rarely shrubs, distributed almost exclusively in the Cerrado, with an important presence in the Espinhaço Range (MacLeish 1987; Loeuille et al. 2019; Alves and Loeuille 2021). They are easily recognizable and generally occur in large populations, being commonly known as “candeias” (loosely translated as lamps) due to their use as fuel (Scolforo et al. 2002; Macedo et al. 2020).

Plants produce several secondary metabolites that have properties of human interest, being potentially exploited by local populations and industries (Briskin 2000; Verma et al. 2012). The overexploitation of biochemical elements in plants has put several species at extinction risk, stimulating studies aimed at the conservation of these species (Rai et al. 2000; Ncube et al. 2011). This has been considered to be one of the major causes of species extinction along with other environmental disturbances, especially plants that are socioeconomically important (Rosser and Mainka 2002; Williams et al. 2014).

Eremanthus species are under constant threat due to intense anthropogenic overexploitation, mainly of *E. erythropappus* and *E. incanus*, which are used locally as fence posts and essential oil extraction by industries, being α-bisabolol the main component (Scolforo et al. 2002; Pádua et al. 2016). α-bisabolol, also known as levomenol, is a monocyclic sesquiterpene alcohol, firstly isolated from chamomile (*Matricaria chamomilla*) in 1951. It has anti-allergic, antibacterial, antiphlogistic, anti-irritant, antimycotic, dermatological, spasmodic and vermifugal properties, being widely used in the cosmetics and pharmaceutical industry.

Eremanthus erythropappus is an important example within the genus with studies that assess the threat and conservation situation and seek solutions to control the overexploitation of the species (Araújo et al. 2018; Pádua et al. 2021). Some studies propose to focus on genetic conservation of species through vegetative propagation methods, maintaining selected genotypes (Fonseca et al. 2021). Population distribution analyses show that over short distances populations are genetically similar and genetic assessments in species populations under anthropogenic influence help to identify priority conservation areas (Pádua et al. 2021). Integrating different methodologies can be very useful in conservation assessment (Peterson 2011; Grossi et al. 2017; Neves et al. 2018).

Some *Eremanthus* species are included in endangered species lists (e.g., Centro Nacional de Conservação da Flora (six species), Lista Oficial das Espécies Endêmicas da Flora Ameaçadas de Extinção do Estado da Bahia (two species) e Lista das Espécies Ameaçadas de Extinção da Flora no Estado de Minas Gerais (two species)). One of the most widely used threatened species classification system is the International Union for Conservation of Nature (IUCN) Red List, which presents categories and criteria that allow an objective evaluation of species extinction risk (IUCN Standards and Petitions Committee 2019). The two most frequently used metrics for assessing species according to the IUCN specifications are the Extent of Occurrence (EOO) and Area of Occupancy (AOO), with many studies using a variety of species distribution modelling methods to calculate EOO and AOO (Marcer et al. 2013; Fivaz and Gonseth 2014; Syfert et al. 2014; Visconti et al. 2016; Breiner et al. 2017; Marco et al. 2018; Moat et al. 2019; Kaky and Gilbert 2019), especially in cases where the data is scarce. The use of Species Distribution Modelling (SDM) in conservation status assessments needs to consider the Minimum Convex Polygon (MCP), which encompass all the predicted habitat areas, to estimate EOO and a grid size of 2 × 2 km to estimate AOO (IUCN Standards and Petitions Committee 2019).

The SDM methodology deals with the formulation of species distribution models presenting possible areas of positive environmental suitability, in agreement with the ecological niche, and based on the combination of current species distribution with environmental variables (Anderson et al. 2003; Elith et al. 2011; Godsoe et al. 2017). There are several applications of predictive species distribution modelling, such as in conservation research that address climate change with the projection of different chronologies, especially future ones (Stockwell and Peterson 2002; Anderson et al. 2003). These methods are used in several fields of biology, such as biogeographic studies, species protection and conservation programs, characterization of degraded areas, recognition of suitable areas for establishment of invasive species and delimitation of priority conservation areas (Araújo and Williams 2000; Peterson and Robins 2003; Engler et al. 2004; Ortega-Huerta and Peterson 2004; Peterson et al. 2006; Siqueira and Durigan 2007; Chen 2009).

Disregarding the interspecific relationships of species and evolutionary adaptations, performing an incomplete sampling of the niche, as well as errors in the data and variables inserted in carrying out the SDM can compromise the results obtained in the analysis and consequently the interpretations (Sinclair et al. 2010). Predictions for the future based on current data could over- or under-estimate species distributions due to uncertainty in projections on how species will respond to climate change and how this will affect the distribution ranges (Thuiller et al. 2008; Fitzpatrick and Hargrove 2009). Extrapolations for different time periods need to consider environmental differences and the equilibrium or not of the species with the environment, which can generate an interpretive risk due to the lack of information on distribution limiting factors and biotic interactions for the past and future (Dormann 2007; Elith and Leathwick 2009).

Another tool that can provide information about species conservation is Gap Analysis (GA), which is largely used in global or local scale and very useful in association with SDM in IUCN red-listing (Grossi et al. 2017). This methodology consists in identifying conservation gaps through the overlapping of data layers of geographical and biotic components, serving as a coarse filter for biodiversity protection (Scott et al. 1993). This analysis shows whether the species are included in Protected Areas (PAs), assessing species distributions according to existing areas under environmental protection policies, providing information about conservation coverage and guiding management actions (Jennings 2000).

This study aims to assess the conservation of all *Eremanthus* species, through the construction of environmental distribution models, application of the IUCN criteria based on records and SDM, and identification of PAs in the distribution models areas. The main questions we intend to answer are: 1) What are the estimated projected environmental suitability areas for the species over time (past, present and future)? 2) Is there a relationship between the Mid-Holocene climatic conditions and the current species distribution? 3) In what proportion are the species included in conservation units? 4) What is the extinction risk classification for the species according to the IUCN criteria? 5) What is the future of species conservation in the face of threats of environmental suitability reduction?

Materials and Methods

Data acquisition

The initial step was to obtain georeferenced data from all species of *Eremanthus* and create a record database. Most of the information was obtained from Benoit Loeuille's personal database, which contains high-quality taxonomic identification data, with support of records stored in the Species Link (http://splink.cria.org.br/) and Global Biodiversity Information Facility (GBIF - https://www.gbif.org/) online databases. After the compilation, the *Eremanthus* database was edited to remove unreliable records, keeping only data suitable for use in research, eliminating problems with misidentification, inaccuracy, records outside raster boundaries, more than one datapoint per pixel and duplicated records (Giannini et al. 2012). This process was carried out manually and with the clean functions ("clean_dupl", "clean_nas", "clean_uni") of the 'modleR' 0.0.0.9000 (Sánchez-Tapia et al. 2018) package in RStudio 1.3.1056 (RStudio Team 2020) with R 3.6.3 (R Core Team 2020), in a two-stage (automatic and manual) cleaning approach (Panter et al. 2020). Only 15 species (*E. capitatus* (Fig. 1b), *E. cinctus, E. crotonoides, E. elaeagnus* (Fig. 1d), *E. erythropappus, E. glomerulatus, E. goyazensis, E. incanus* (Fig. 1c), *E. mattogrossensis, E. mollis, E. polycephalus, E. reticulatus, E. rondoniensis, E. syncephalus, E. uniflorus*) were included in this study, because the other eight species (*E. arboreus, E. argenteus, E. auriculatus, E. brevifolius, E. hatschbachii, E. ovatifolius, E. praetermissus, E. veadeiroensis*) have less than 10 records in the database.

Species Distribution Modelling

SDM was performed using the 'modleR' package in RStudio. Brazil was the main study area, except for *E. cinctus, E. mattogrossensis* and *E. rondoniensis,* for which Brazil and Bolivia were used as base area, as there was suspicion from preliminary modelling tests that an area of suitability for *E. cinctus* could be present in Bolivia and because the other two species occur in both countries. Nineteen bioclimatic variables were obtained from the WorldClim version 1.4 database (Hijmans et al. 2005) with 2.5 minutes spatial resolution. The Global Climate Model (GCM) used was the Model for Interdisciplinary Research on Climate-Earth System Model (MIROC-ESM). To apply in the analysis, these variables were cropped through 'raster' package in RStudio using the previously described study area as base (Hijmans 2021).

The selection of the bioclimatic variables for modelling was performed with the 'modleR' package. Correlated variables were excluded, maintaining the bioclimatic variables Mean Diurnal Range (Mean of monthly (max temp – min temp)), Isothermality, Mean Temperature of Wettest Quarter, Mean Temperature of Warmest Quarter, Precipitation of Wettest Month, Precipitation Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter, Precipitation of Warmest Quarter and Precipitation of Coldest Quarter. The modelling was carried out for the present (1960-1990) and projected to the past in the Mid-Holocene (~6000 years ago) and to the future in 2070 with all Representative Concentration Pathways (RCPs) scenarios (2.6, 4.5, 6.0 and 8.5), to visualize the range of suitable areas for species occupation through time. Past models had the purpose of elucidating the history of environmental suitability in *Eremanthus* from an OSL perspective and to identify possible influence on the current and future distributions. To maintain consistency with other analyses and avoid confusion, RCP 8.5 was maintained as a reference in the presentation of results and discussion. Maxent and Bioclim were the algorithms used for modelling and the models used in this study are an ensemble of both, based on models with True Skill Statistics (TSS) value above 0.7.

IUCN Red List assessment

The recommendations in the Guidelines for Application of IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2019) demonstrate how to carry out EOO and AOO calculations, including cases of spatially predicted sites. Furthermore, SDM models need to be binarized through a threshold value before these calculations. The thresholds must be properly established because they directly affect the coverage of suitable habitats in the binarized models and, consequently, the species status assessment (Liu et al. 2005, 2016).

The species classification method for IUCN red-listing followed the parameters established by the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2001, 2012) and Guidelines for Application of IUCN Red List Categories and Criteria Version 14 (IUCN

Standards and Petitions Committee 2019). The species were submitted to criterion B, which refers to the limitation of geographic distribution, and to subcriterion (b), referring to continuous decline. No analyses were carried out to enable the classification of species in subcriteria (a) and (c), which deal with severely fragmented populations and extreme fluctuations in populations, respectively. According to the IUCN provisions, to determine that a species is fully classified in criterion B, the assessed species must also meet the requirements of at least two of the three previously mentioned subcriteria. Therefore, the results of the assessment of *Eremanthus* species based on the IUCN criteria are presented in a preliminary way. Notwithstanding, in the face of worsening imminent environmental threats worldwide, this study presents consistent and important preliminary results that will serve as basis for a classification that completely fulfils the IUCN Red List requirements.

The letters “f”, “h”, “l”, “p”, “r” and “t”, when mentioned together with EOO and AOO, are abbreviations for “future”, “hull” (referring to convex hull/MCP), “loss”, “present”, “records” and “total” (referring to total area), respectively. To evaluate *Eremanthus* species according to the IUCN specifications for criterion B, individual records were used to calculate EOOr (criterion B1), through MCP, and AOOr (criterion B2), using the 2 × 2 km (4 km^2) reference scale for grid size. EOO and AOO of SDM models of the present (EOOp and AOOp) and of the future with RCP 8.5 (EOOf and AOOf) were calculated, as well as their respective values within the MCP (EOOph, AOOph, EOOfh and AOOfh), in order to identify a possible decline of a species in the projections. To perform such calculations, SDM models were binarized (i.e., areas with environmental suitability received a value of 1 and areas without environmental suitability received a 0 value) by obtaining the threshold values when the Minimal Predicted Area (MPA) with 90% of the species records was applied, in order to avoid any possible remaining incorrect records and ensure the reliability of the records in the analysis. With these binary models representing the potential habitat area, the area of occupied habitat was estimated and EOOp, AOOp, EOOf, AOOf, EOOph, AOOph, EOOfh and AOOfh were calculated. These procedures were carried out in the R packages ‘ecospat’ (Broennimann et al. 2020) and ‘red’ (Cardoso 2020).

Gap Analysis

The previously generated binarized models were used as basis for GA calculation. This enables greater parameterization of the analysis and higher fidelity in result comparison, in addition to ensuring more reliable results, as the binary models follow a calculated threshold.

The anthropized areas (BDiA 2020) were removed from the binarized models to avoid inserting areas where the species certainly do not occur, i.e., only suitable areas with anthropogenic absence were used in the analysis. The layers resulting from this process were overlapped with the PAs (ICMBio 2020), and PAs occurring in suitable areas were identified and extracted. The percentage of protected areas within the environmental suitability area for each species was then calculated. The next step was to identify which species are present within PAs and calculate how many records represent the presence of the species in these areas. All these procedures were performed in the software QGIS 3.12.0 (QGIS Development Team 2020).

Cartographical procedures

E. erythropappus was selected as an example to cartographically represent the results obtained here, as it is the better known and exploited *Eremanthus* species. Maps representing the results for other *Eremanthus* species are available in the Online Resource 1-45. Maps were designed using the software QGIS 3.12.0, using the data generated in the previous analyses.

Results

SDMs and environmental suitability

The models resulting from the SDM showed satisfactory results. With the exception of *Eremanthus capitatus* and *E. crotonoides*, the environmental suitability of the species in the models corresponding to the Mid-Holocene period showed similar and reduced areas compared to the SDM environmental suitability results for the present (see electronic supplementary material). *E. capitatus* showed a more extensive area of suitability in the past when compared to the present, especially on the eastern Brazilian coast between the states of Bahia and Rio de Janeiro (Online Resource 1, 2). Similarly, when compared to the models based upon data for the present, *E. crotonoides* demonstrated to have a greater suitability on the coast from north-eastern São Paulo to southern Bahia and also on the northern portion of the state of São Paulo in the Mid-Holocene period (Online Resource 7, 8).

The SDM results for the present were consistent with the records, showing wider areas of suitability in relation to the current distribution of the species and in agreement with the Cerrado. The Espinhaço Range was the region which more frequently appeared in the models as an area conducive to the establishment of the species, especially the Espinhaço Meridional, including for *Eremanthus cinctus* (Online Resource 5), *E. goyazensis* (Online Resource 20), *E. mattogrossensis* (Online Resource 26), *E. mollis* (Online Resource 29) and *E. uniflorus* (Online Resource 44), which currently do not have records in this geological formation. The Eastern Cordillera in Bolivia was an important present area of suitability in the models of *E. cinctus*, *E. mattogrossensis* and *E. rondoniensis*, with the exception of *E. cinctus* in the future and *E. mattogrossensis* in Mid-Holocene simulations, which did not show significant suitability in that region (Online Resource 4-6, 25-27, 37-39). *E. mattogrossensis* showed a large variation in SDM results in the three time periods, presenting disjunct areas in the Mid-Holocene in the Espinhaço Range, Planalto dos Guimarães, surroundings of Chapada dos Parecis and Depressão da Amazônia Meridional, a wider suitability in the present, and high reduction in suitability estimated for the future (Online Resource 25-27).

In relation to the results presented by the future SDM models, a great decrease in the environmental suitability area was observed for all species in all RCP scenarios when compared to the present models. The loss of suitability between models at the different RCP levels was relatively similar and with a gradual increase from the RCP 2.6 level (more optimistic scenario) to the RCP 8.5 level (more pessimistic scenario). Almost all species showed decrease of suitability area to a very reduced region between the states of Minas Gerais, Rio de Janeiro and São Paulo, especially in areas of Serra da Mantiqueira and Serra do Mar (see electronic supplementary material). *E. cinctus* (Online Resource 6), *E. goyazensis* (Online Resource 21), *E. mollis* (Online Resource 30) and *E. uniflorus* (Online Resource 45) show a trend to disappear from the current distribution areas, with a more critical situation for the latter, which will practically lose the entire adequacy area where current records are located. The Cordillera Oriental showed a high level of suitability in the future projection of *E. rondoniensis*, while the areas of suitability in Brazil were significantly reduced (Online Resource 39). The future projection of *E. capitatus* showed a great extent of adequacy area, however, with a low adequacy index for the most part (Online Resource 3).

Eremanthus erythropappus presented well-marked and similar areas of environmental suitability for the Mid-Holocene and the present (Figs. 2, 3). In the past, the species distribution estimative was restricted to Espinhaço Meridional, Serra da Mantiqueira, Serra do Mar and Serra da Canastra, while the present model highlighted the same regions with a small increase in the area of environmental suitability towards Brasília. Projections for the future estimate a drastic reduction in the suitability area of about 75% compared to the present, with restriction to the northeast portion of São Paulo, Serra da Mantiqueira and Serra do Mar (Fig. 4, Table 1).

Gap Analysis: Records and PAs

Present

With the exception of *E. uniflorus*, all other species presented less than 50% of their records within PAs (Table 1). The highest and lowest percentage of records in PAs were found in *E. uniflorus* (72%) and *E. cinctus* (8%), respectively. All species showed low percentages of PAs in areas of suitability, with values between 12% (*E. mattogrossensis*) and 27% (*E. erythropappus*) and the majority presenting values below 25%. The average percentage of records in PAs was 31% and the average percentage of suitability areas contained in PAs was 18% (Table 1).

Future

The results presented here reflect a stationary condition of the PAs. In view of changes in circumscription of PAs caused by climate change and public policies, the future GA values can be different. *Eremanthus cinctus*, *E. crotonoides*, *E. erythropappus*, *E. incanus* and *E. mollis* showed percentage values of PAs in suitability areas greater than 50% (60%, 61%, 68%, 54% and 56%, respectively). The other species showed values between 25% (*E. rondoniensis*) and 49% (*E. glomerulatus*), with an average percentage of 46%. The projected percentages of suitability area loss and PA loss in relation to suitability areas were evaluated. The lowest and highest percentages of suitability area loss were 51% for *E. rondoniensis* and 97% for *E. mattogrossensis*, with an average value of 82% among all species. *Eremanthus uniflorus* and *E. rondoniensis* presented the highest and lowest percentage values of PA loss with 93% and 2%, respectively, and the average among all species was 59% (Table 1).

EOO, AOO and IUCN red listing

Consistent values of EOO and AOO were obtained in all situations defined for this study. The values found for AOOr were sufficient to fit the species in the requirements of IUCN criterion B (Table 2). The EOOp, AOOp, EOOf, AOOf, EOOph, AOOph, EOOfh and AOOfh results allowed us to identify a projected decline in EOO and AOO, due to the difference between present and future values. All species presented considerable EOO and AOO losses. The projections show an average percentage of total area EOO and AOO loss (EOOtl and AOOtl) of 60% and 83%, respectively, and of 71% and 89% for the area belonging to MCP records (EOOhl and AOOhl), respectively.

When it comes to EOOf and AOOf, only *E. uniflorus* fits IUCN criterion B parameters, however, the situation considerably changes when EOOfh and AOOfh are used. In this case, *E. cinctus*, *E. goyazensis*, *E. mollis* and *E. uniflorus* fit the geographic limitation criterion for both measurements, while *E. elaeagnus*, *E. polycephalus* and *E. syncephalus* are classified under the same criterion only with AOOfh values. In this situation, *E. cinctus* and *E. uniflorus* are the most critical cases, with total absence of these two species within the areas of the convex hull of records in future estimates.

EOOr, EOOp, AOOp, EOOph and AOOph results were not significant for classification under IUCN criterion B. Thus, the species of the *Eremanthus* classified in IUCN criterion B2b(i,ii), considering AOOr results and the projected EOO and AOO reductions were *E. capitatus, E. crotonoides, E. erythropappus, E. glomerulatus* and *E. incanus* in the Vulnerable (VU) category and *E. cinctus, E. elaeagnus, E. goyazensis, E. mattogrossensis, E. mollis, E. polycephalus, E. reticulatus, E. rondoniensis, E. syncephalus* and *E. uniflorus* in the Endangered (EN) category (Table 2). Currently, IUCN presents a conservation status classification for *E. cinctus, E. elaeagnus, E. erythropappus E. glomerulatus, E. goyazensis, E. incanus, E. mattogrossensis* and *E. uniflorus* in the Least Concern (LC) category, for *E. auriculatus* and *E. praetermissus* in the Vulnerable (VU) category, for *E. argenteus, E. leucodendron* and *E. veadeiroensis* in the Endangered (EN) category and for *E. brevifolius* and *E. ovatifolius* in the Critically Endangered (CR) category. CNCFlora classifies *E. capitatus* and *E. crotonoides* as LC, *E. argenteus* and *E. leucodendron* as EN and *E. polycephalus* and *E. seidelii* (= *E. elaeagnus*) as VU (Martinelli and Moraes 2013).

Discussion

The application of SDM methods facilitates understanding the relationship between species geographical distribution and ecological niche, considering biotic, abiotic and distribution factors (Peterson et al. 2011). The use of SDM is recommended in studies proposing conservation-oriented decision making, such as ours, contributing to direct actions (Guisan et al. 2013).

The similarities found between Mid-Holocene palaeomodels and models for the present in the SDM results show a pattern of environmental stability in several areas of the Espinhaço Range (e.g., Diamantina Plateau and Serra do Cipó), Serra da Canastra and mountainous regions from Goiás, which corroborate to the OSLs and reinforce the importance of the environmental stability during the process of contractions and expansions of high altitude vegetation (Barbosa 2011; Bitencourt and Rapini 2013; Barres et al. 2019; Rapini et al. 2021). Several studies have shown the importance of Espinhaço Meridional as the main area of endemism and centre of origin for several campos rupestres plant species in the Espinhaço Range, further corroborating the importance of this mountainous formation as shown in *Eremanthus* SDM (Echternacht et al. 2011; Inglis and Cavalcanti 2018; Alves and Loeuille 2021). The occurrence of several *Eremanthus* species in high altitude campos rupestres areas is likely due to climatic fluctuations during the Holocene and previous geological periods (Silva et al. 2020). Expansions and contractions of specific vegetation types resulted in the establishment of campos rupestres as one of the typical altitude vegetation in Brazil (Barbosa 2011).

The distribution of *Eremanthus* species could have been influenced by the warm and dry climates that predominated in the Mid-Holocene, with the past SDM presenting suitability conditions similar to the present ones (Steig 1999; Behling 2002; Wanner et al. 2008; Bitencourt and Rapini 2013). Our results are thus consistent with the OSL theory, in which the presence of climatically stable areas for long periods of time promoted genetic isolation of *Eremanthus* populations and consequent speciation, favouring endemism (Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Silveira et al. 2016; Fiorini et al. 2019). Other studies using SDM with other plant families, such as the locally diverse Velloziaceae and Bromeliaceae, obtained similar results, giving further evidence of the stability of OSL areas, especially in campos rupestres (Hmeljevski et al. 2017; Fiorini et al. 2019; Vidal et al. 2019; Cortez et al. 2020).

Considering the current occurrence records, the high density of botanical collections from the Espinhaço Range and the SDM simulations, it is unlikely that *E. cinctus* (Online Resource 4, 5), *E. goyazensis* (Online Resource 19, 20), *E. mattogrossensis* (Online Resource 25, 26), *E. mollis* (Online Resource 28, 29) and *E. uniflorus* (Online Resource 43, 44) have occupied this mountain range in the past, but unidentified biotic and/or abiotic dispersion barriers may have kept the species away from this area (Alves and Loeuille 2021). The environmental suitability of the Espinhaço Range for *E. elaeagnus* (Online Resource 10, 11), *E. incanus* (Online Resource 22, 23), *E. polycephalus* (Online Resource 31, 32), *E. reticulatus* (Online Resource 34, 35) and *E. syncephalus* (Online Resource 40, 41) occurred nearly exclusively during the Mid-Holocene, posteriorly advancing through the Brasília Arch (mountainous formations extending from the southern limit of the Espinhaço Range, passing through Serra da Canastra and heading towards Chapada dos Veadeiros). Few records of *E. incanus*, *E. reticulatus* and *E. syncephalus* are found in the Brasília Arch, mostly concentrated in the Espinhaço Meridional, suggesting a recent occupation of the Brasília Arch. According to the simulations, we can assume that the climatic changes after the Mid-Holocene increased the environmental suitability for *E. mattogrossensis* (Online Resource 25-27), allowing a connection between previously separated areas of suitability and generating favourable conditions for range expansion (Steig 1999; Behling 2002; Wanner et al. 2008).

The SDM models for present environmental suitability showed that high elevation regions corresponding to the Espinhaço Range campos rupestres are important areas for *Eremanthus*, even though species do not have current records in these locations. The Espinhaço Meridional presents higher environmental suitability in comparison to the Espinhaço Septentrional and Chapada Diamantina. The Brasília Arch also is an important area of suitability, as it houses records for some species and presents potential conditions for establishment of *Eremanthus* species. Planalto da Diamantina and Serra do Cipó, widely recognized as areas of intense research, hosting national parks focused on campos rupestres conservation, are other important regions highlighted by the modelling (Rapini et al. 2008; Alves and Loeuille 2021).

The GA and SDM results show that strong anthropogenic presence affect most areas of suitability in the SDM models (see electronic supplementary material). Most species of *Eremanthus* are distributed in small areas immersed in a high demographic density matrix, limiting the areas where they can establish and contributing to the intensification of population restriction (Mcdonald et al. 2008, 2009). Conservation units constitute a very low percentage in areas of suitability for *Eremanthus*, increasing the possibility of species disappearing from the natural environment as anthropogenic occupation becomes more intense in unprotected areas (Rapini et al. 2008; Mcdonald et al. 2009). Fragmented areas with limited environmental suitability and threatened by anthropogenic activities (e.g., mining, fires, agriculture, livestock, urban expansion, exotic and invasive species, extraction of non-timber products) is also a problem to other groups, such as *Espeletia* (Asteraceae) that occur in mountainous Andean areas in the Páramo heterogeneous habitats (Valencia et al. 2020).

Among the species studied here, *Eremanthus erythropappus* is the one subjected to greater anthropogenic threats, due to indiscriminate wood extraction, being the subject of several conservation studies (Scolforo et al. 2002; Pádua et al. 2016) (Fig. 1e). *E. erythropappus* is commonly found in soils with high heavy metal concentrations, with implications to implementation of revegetation measures, in addition to sustainable management projects (Machado et al. 2013; Araújo et al. 2018). Population genetics studies are important to understand microevolutionary processes that can influence in the conservation of species like *E. erythropappus*, informing how populations should be managed. Studies of functional traits can show how the environment promotes variation in the species morphology (Borges et al. 2018; Rocha et al. 2020a, b). A concerted effort between the government, the private sector and the society is needed for the preservation of this species, which otherwise will likely disappear from nature (Carvalho et al. 2019).

The future projections show a dire scenario. The expected suitability areas for *Eremanthus* are very small, and some species will likely become extinct in the natural environment, such as *E. uniflorus* (Online Resource 45). Additionally, these areas present a much lower potential for suitability when considering the GA results, further aggravating the situation, as PAs might not be effective to protect species, due to the reduced percentage of records in them (Oliveira et al. 2017). It is likely that many species of *Eremanthus* will not be able to reach areas of future suitability and establish in the areas identified by GA, as these favourable suitability areas are in regions with high levels of anthropogenic activity and few preserved areas (Mcdonald et al. 2009). Given that our results consider the current situation of anthropogenic areas and conservation units in the future projections, the conservation situation of *Eremanthus* species is expected to become more critical in the coming decades. A common issue for species likely to be subjected to future distribution restrictions is AOO volatility, i.e., differences in species distribution along time in restricted and environmentally impacted areas cause an oscillation of the future estimated AOO (Marco et al. 2018).

Our study presents similar results to those of Carvalho et al. (2019), especially in the drastic reduction of projected future suitability areas, requiring immediate conservation actions, as they show a restriction of the distribution to the regions of Serra da Mantiqueira and Serra do Mar, and disappearance in several areas where it is currently distributed (Figs. 3, 4). We also obtained similar results to those of Bitencourt et al. (2016), with the majority of the suitability areas for campos rupestres in the Espinhaço Range but also in other areas such as Serra da Canastra (Minas Gerais state) and Chapada dos Veadeiros (Goiás state), projection of great loss of suitability area (including the few PAs of the Espinhaço Range) with the campos rupestres almost exclusive in the Espinhaço Meridional (barely present in the northern and outside of the Espinhaço Range) and a high potential of species extinction in campos rupestres due to habitat loss. A small number of endemic species is protected by PAs and many of these areas may become less effective due to climate change, therefore, conservation actions need to consider the representativeness and ecology of the species (Bitencourt et al. 2016). The presence of *Eremanthus* in PAs is also low and can be affected by the climate change in the coming decades.

When estimating areas of suitability using quantitative values, SDM serves as an objective resource in IUCN assessments that aim to understand the relationship of the species with the environment (Sangermano and Eastman 2012). The integrative application of SDM, GA and IUCN red listing allows the visualization of the current distribution of the species and their future behaviour in face of environmental conditions, in addition to contributing to conservation management by identifying the percentage of PAs within EOO and AOO (Marcer et al. 2013). These results can serve as a basis for planning conservation strategies with greater preparation and effectiveness, especially when it comes to developing countries where research is scarce (Fivaz and Gonseth 2014). Reliable results are obtained when measurements of EOO and AOO are performed using SDM models in a careful approach (Kaky and Gilbert 2019).

The use of SDM as a tool for classifying *Eremanthus* species in IUCN criterion B2b(i,ii) was effective, especially regarding the assessment of species spatial distribution and the future behaviour of EOO and AOO in relation to extinction risks (Kaky and Gilbert 2019). SDM showed a projected decline for EOO and AOO, both being essential components for IUCN classification (IUCN Standards and Petitions Committee 2019). The results showed that AOOr values were essential to classify *Eremanthus* species in threatened species lists, as none of the EOOr results met IUCN requirements (Kaky and Gilbert 2019). When comparing EOOph, AOOph, EOOfh and AOOfh with EOOp, AOOp, EOOf and AOOf it is evident that the manner in which the MCP of the SDM models is delimited greatly influences results, when considering the criterion B parameters (Fivaz and Gonseth 2014).

Although our methodological approaches were positively integrated in the results, some issues need to be noted. SDM can generate a wide range of models with different environmental suitability probabilities, therefore, it must be carefully prepared and evaluated, especially regarding the choice of environmental layers, which should consider the actual condition of the species (Fivaz and Gonseth 2014; IUCN Standards and Petitions Committee 2019). Depending on the level of the RCP used for the future projections, the generated models can result in conflicting environmental suitability conditions that can directly influence other analyses (Moat et al. 2019; Kaky and Gilbert 2019). The use of different algorithms can also influence research results and interpretations and should be chosen appropriately (Elith and Leathwick 2009). The two-stage cleaning approach of database records is essential for result credibility and accuracy, especially in species extinction risk assessment (Panter et al. 2020). The records should be properly filtered to eliminate possible errors, as the geographic location of the species directly influences MCP, EOO and AOO values and consequently the fitting of the species in IUCN red list categories (Fivaz and Gonseth 2014). Additionally, the effects of species sampling on SDM performance and accuracy and the use of statistical evaluation criteria for the models should be considered (Stockwell and Peterson 2002; Allouche et al. 2006; Wisz et al. 2008).

The absence of data in the SDM that portray the species biotic factors compromises the real prospects of how species can overcome environmental threats, especially in future estimates as the effects and constraints of these biotic relationships can be ignored (Elith and Leathwick 2009; Sinclair et al. 2010). Populations and species are subject to the consequences of natural selection, contributing to the reduction of the risk of extinction of species as they can adapt to environmental changes even in scenarios of accelerated modification (Etterson and Shaw 2013; Fox et al. 2019; Bemmels and Anderson 2019). SDM models may overestimate environmental losses and species extinctions by not considering potential genetic adaptations in response to environmental changes, and incorporating genomic data into the analysis may increase the reliability of the results (Razgour et al. 2019). Inclusion of approaches involving evolutionary processes and local adaptations of species in the SDM demonstrate that the risks of environmental vulnerability presented in the models are reduced, which contribute significantly for a better species dynamic interpretation (Bush et al. 2016; Peterson et al. 2019; Chen et al. 2020). The factors mentioned above, along with other variables such as migration, genetic drift and population dynamics, contribute to the change in species distributions of future predictions, since these factors are dynamic, unpredictable and can be incorporated into the SDM, generating different interpretations (Bush et al. 2016; Razgour et al. 2019).

It is important to highlight that anthropogenic threats continue to intensify in Cerrado and campos rupestres areas, mainly due to mining, which drastically changes the natural landscape by modifying the relief, removing soil and vegetation, the use of alien grasses for pasture and deforestation caused by agriculture expansion (Ratter et al. 1997; Pivello et al. 1999; Pena et al. 2017). Some habitat recovery initiatives have been implemented over the years, however, restoring the natural conditions of botanical communities is difficult and further impaired by the threat of ruderal invasive species (Silveira et al. 2016). OSLs are extremely important for global biodiversity and the Brazilian savannas are especially important in this context: they harbour thousands of endemic species resulting from a long historical process and are in serious risk of disappearing in the coming decades due to slowness of conservation actions (Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Silveira et al. 2016). Few protection areas are located in OSLs areas in Brazil and the low representation of endangered species in these areas reinforce the idea that PAs are not effective in protecting biodiversity (Françoso et al. 2015; Neves et al. 2018).

The results presented here are positive from the perspective of their applicability as a scientific contribution and, along with previous research, reinforces the pertinence of SDM for application of IUCN Red List Criteria (Marcer et al. 2013; Fivaz and Gonseth 2014; Syfert et al. 2014; Marco et al. 2018; Moat et al. 2019; Kaky and Gilbert 2019). Future study that investigates the populational dynamics of *Eremanthus* may be the path to complete the necessary requirements for including species of the genus in IUCN Red List Criteria. The application of SDM in paleoclimates anterior to the Mid-Holocene (e.g., Last Glacial Maximum and Last Inter-Glacial) can bring important information about distribution cycles in the genus and the possible implications for present and future species distribution.

Conclusions

Due to the Mid-Holocene climatic changes, and possibly from previous periods, the campos rupestres and Cerrado areas underwent expansion and contraction processes that probably resulted in changes in the geographic distribution of *Eremanthus* species. Present and future suitability areas found in the SDM allowed to identify regions for species establishment, however, a significant part of these areas has some degree of anthropogenic interference. As a consequence, a small percentage of the suitability areas is actually available for species occupation, with an even smaller fraction of these areas within PAs, which explains the current low proportion of species records in conservation units. The future prospects dire in relation to species sustainability in nature. Thus, classifying threatened species using the IUCN Red List criteria, even if partially, is essential for the elaboration of strategies for preparation and application of conservation-oriented policies and prevention of environmental damage. The Espinhaço Range, core area of the *Eremanthus* distribution, harbour several threatened plant groups in an important physiognomy that needs to be better scientifically understood for preservation purposes. The results obtained through integration of different methodologies provide the basic framework for their application in conservation models.

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References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Alves FVS, Loeuille BFP (2021) Geographic distribution patterns of species of the subtribe Lychnophorinae (Asteraceae: Vernonieae). Rodriguésia 72:e02072019.2021. https://doi.org/10.1590/2175-7860202172072

Alves RJV, Silva NG, Oliveira JA, Medeiros D (2014) Circumscribing campo rupestre – megadiverse Brazilian rocky montane savanas. Brazilian Journal of Biology 74:355–362. https://doi.org/10.1590/1519-6984.23212

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162:211–232. https://doi.org/10.1016/S0304-3800(02)00349-6

Araújo EJG de, Netto SP, Scolforo JRS, et al (2018) Sustainable Management of Eremanthus erythropappus in Minas Gerais, Brazil – A Review. Floresta e Ambiente 25:e20160516. https://doi.org/10.1590/2179-8087.051616

Araújo MB, Williams PH (2000) Selecting areas for species persistence using occurrence data. Biological Conservation 96:331–345. https://doi.org/10.1016/S0006-3207(00)00074-4

Barbosa NPU (2011) Modelagem de Distribuição Aplicada aos Campos Rupestres. Doctoral dissertation, Universidade Federal de Minas Gerais

Barres L, Batalha-Filho H, Schnadelbach AS, Roque N (2019) Pleistocene climatic changes drove dispersal and isolation of Richterago discoidea (Asteraceae), an endemic plant of campos rupestres in the central and eastern Brazilian sky islands. Biological Journal of the Linnean Society 189:132–152. https://doi.org/10.1093/botlinnean/boy080

BDiA (2020) Banco de Dados de Informações Ambientais. https://bdiaweb.ibge.gov.br/#/consulta/vegetacao. Accessed 20 May 2022

Behling H (2002) South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecology 177:19–27. https://doi.org/10.1016/S0031-0182(01)00349-2

Bemmels JB, Anderson JT (2019) Climate change shifts natural selection and the adaptive potential of the perennial forb Boechera stricta in the Rocky Mountains. Evolution (N Y) 73:2247–2262. https://doi.org/10.1111/evo.13854

Bitencourt C, Rapini A (2013) Centres of endemism in the espinhaço range: Identifying cradles and museums of asclepiadoideae (apocynaceae). Systematics and Biodiversity 11:525–536. https://doi.org/10.1080/14772000.2013.865681

Bitencourt C, Rapini A, Santos Damascena L, de Marco Junior P (2016) The worrying future of the endemic flora of a tropical mountain range under climate change. Flora - Morphology, Distribution, Functional Ecology of Plants 218:1–10. https://doi.org/10.1016/j.flora.2015.11.001

Borges ER, Prado-Junior J, Santana LD, et al (2018) Trait variation of a generalist tree species (Eremanthus erythropappus, Asteraceae) in two adjacent mountain habitats: Savanna and cloud forest. Australian Journal of Botany 66:640–646. https://doi.org/10.1071/BT18114

Breiner FT, Guisan A, Nobis MP, Bergamini A (2017) Including environmental niche information to improve IUCN Red List assessments. Diversity and Distributions 23:484–495. https://doi.org/10.1111/ddi.12545

Briskin DP (2000) Update on Phytomedicines Medicinal Plants and Phytomedicines. Linking Plant Biochemistry and Physiology to Human Health. Plant Physiology 124:507–514. https://doi.org/10.1104/pp.124.2.507

Broennimann O, di Cola V, Guisan A (2020) ecospat: Spatial Ecology Miscellaneous Methods. R package version 3.1.

Bush A, Mokany K, Catullo R, et al (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19:1468–1478. https://doi.org/10.1111/ele.12696

Cardoso P (2020) red: IUCN Redlisting Tools. R package version 1.5.0.

Carvalho MC, Gomide LR, Acerbi FW, Tng D (2019) Potential and future geographical distribution of Eremanthus erythropappus (DC.) MacLeish: A tree threatened by climate change. Floresta e Ambiente 26:e20180455. https://doi.org/10.1590/2179-8087.045518

Chen Q, Yin Y, Zhao R, et al (2020) Incorporating Local Adaptation Into Species Distribution Modeling of Paeonia mairei, an Endemic Plant to China. Frontiers in Plant Science 10:1717. https://doi.org/10.3389/fpls.2019.01717

Chen Y (2009) Conservation biogeography of the snake family Colubridae of China. Journal of Zoology 5:251–262

Colli GR, Vieira CR, Dianese JC (2020) Biodiversity and conservation of the Cerrado: recent advances and old challenges. Biodiversity and Conservation 29:1465–1475. https://doi.org/10.1007/s10531-020-01967-x

Colli-Silva M, Vasconcelos TNC, Pirani JR (2019) Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. Journal of Biogeography 46:1723–1733. https://doi.org/10.1111/jbi.13585

Cortez MB de S, Folk RA, Grady CJ, et al (2020) Is the age of plant communities predicted by the age, stability and soil composition of the underlying landscapes? An investigation of OCBILs. Biological Journal of the Linnean Society 1–20. https://doi.org/10.1093/biolinnean/blaa174/5957421

Dormann CF (2007) Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8:387–397. https://doi.org/10.1016/j.baae.2006.11.001

Echternacht L, Trovó M, Oliveira CT, Pirani JR (2011) Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil. Flora: Morphology, Distribution, Functional Ecology of Plants 206:782–791. https://doi.org/10.1016/j.flora.2011.04.003

Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith J, Phillips SJ, Hastie T, et al (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Engler R, Guisan A, Rechsteiner L (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology 41:263–274. https://doi.org/10.1111/j.0021-8901.2004.00881.x

Etterson JR, Shaw RG (2013) Evolution in Response to Climate Change. In: Encyclopedia of Biodiversity: Second Edition. Elsevier Inc., pp 385–391

Fernandes GW, Arantes-Garcia L, Barbosa M, et al (2020) Biodiversity and ecosystem services in the Campo Rupestre: A road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspectives in Ecology and Conservation. https://doi.org/10.1016/j.pecon.2020.10.004

Fiorini CF, Miranda MD, Silva-Pereira V, et al (2019) The phylogeography of Vellozia auriculata (Velloziaceae) supports low zygotic gene flow and local population persistence in the campo rupestre, a Neotropical OCBIL. Botanical Journal of the Linnean Society 191:381–398. https://doi.org/10.1093/botlinnean/boz051

Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the problem of non-analog climate. Biodiversity and Conservation 18:2255–2261. https://doi.org/10.1007/s10531-009-9584-8

Fivaz FP, Gonseth Y (2014) Using species distribution models for IUCN Red Lists of threatened species. Journal of Insect Conservation 18:427–436. https://doi.org/10.1007/s10841-014-9652-6

Fonseca ALC, Magalhães TA, Melo LA, et al (2021) Rescue and vegetative propagation of Eremanthus erythropappus (DC.) MacLeish in natural stand. Brazilian Journal of Biology 81:566–574. https://doi.org/10.1590/1519-6984.225119

Fox RJ, Donelson JM, Schunter C, et al (2019) Beyond buying time: The role of plasticity in phenotypic adaptation to rapid environmental change. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20180174. https://doi.org/10.1098/rstb.2018.0174

Françoso RD, Brandão R, Nogueira CC, et al (2015) Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. Natureza e Conservação 13:35–40. https://doi.org/10.1016/j.ncon.2015.04.001

Giannini TC, Siqueira MF, Acosta AL, et al (2012) Desafios atuais da modelagem preditiva de distribuição de espécies. Rodriguésia 63:733–749. https://doi.org/10.1590/S2175-78602012000300017

Godsoe W, Franklin J, Blanchet FG (2017) Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. Ecology and Evolution 7:654–664. https://doi.org/10.1002/ece3.2657

Grossi MA, Draper D, Apodaca MJ, et al (2017) The road to 2020 targets and the learnings from the emblematic South American plant genus Nassauvia (Asteraceae). Biodiversity and Conservation 26:329–351. https://doi.org/10.1007/s10531-016-1245-0

Guisan A, Tingley R, Baumgartner JB, et al (2013) Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435. https://doi.org/10.1111/ele.12189

Hijmans RJ (2021) raster: Geographic Data Analysis and Modeling. R package version 3.4-10

Hijmans RJ, Cameron SE, Parra JL, et al (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978. https://doi.org/10.1002/joc.1276

Hmeljevski KV, Nazareno AG, Leandro Bueno M, et al (2017) Do plant populations on distinct inselbergs talk to each other? A case study of genetic connectivity of a bromeliad species in an Ocbil landscape. Ecology and Evolution 7:4704–4716. https://doi.org/10.1002/ece3.3038

Hopper SD (2009) OCBIL theory: Towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant and Soil 322:49–86. https://doi.org/10.1007/s11104-009-0068-0

Hopper SD, Lambers H, Silveira FAO, Fiedler PL (2021) OCBIL theory examined: reassessing evolution, ecology and conservation in the world’s ancient, climatically buffered and infertile landscapes. Biological Journal of the Linnean Society 133:266–296. https://doi.org/10.1093/biolinnean/blaa213

Hopper SD, Silveira FAO, Fiedler PL (2016) Biodiversity hotspots and Ocbil theory. Plant and Soil 403:167–216. https://doi.org/10.1007/s11104-015-2764-2

ICMBio (2020) Mapa Temático e Dados Geoestatísticos das Unidades de Conservação Federais. https://www.gov.br/icmbio/pt-br/servicos/geoprocessamento/mapa-tematico-e-dados-geoestatisticos-das-unidades-de-conservacao-federais. Accessed 20 May 2022

Inglis PW, Cavalcanti TB (2018) A molecular phylogeny of the genus diplusodon (Lythraceae), endemic to the campos rupestres and cerrados of South America. Taxon 67:66–82. https://doi.org/10.12705/671.5

IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1., 1st edn. IUCN Species Survival Commission, Gland, Switzerland

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1., 2nd edn. IUCN Species Survival Commission, Gland, Switzerland

IUCN Standards and Petitions Committee (2019) Guidelines for Using the IUCN Red List Categories and Criteria, Version 14. Standards and Petitions Committee of the IUCN Species Survival Commission, Gland, Switzerland

Jennings MD (2000) Gap analysis: concepts, methods, and recent results. Landscape Ecology 15:5–20. https://doi.org/10.1023/A:1008184408300

Kaky E, Gilbert F (2019) Assessment of the extinction risks of medicinal plants in Egypt under climate change by integrating species distribution models and IUCN Red List criteria. Journal of Arid Environments 170:103988. https://doi.org/10.1016/j.jaridenv.2019.05.016

Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. Conservation Biology 19:707–713. https://doi.org/10.1111/j.1523-1739.2005.00702.x

Lenthall JC, Bridgewater S, Furley PA (1999) A phytogeographic analysis of the woody elements of New World savannas. Edinburgh Journal of Botany 56:293–305. https://doi.org/10.1017/S0960428600001153

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Liu C, Newell G, White M (2016) On the selection of thresholds for predicting species occurrence with presence-only data. Ecology and Evolution 6:337–348. https://doi.org/10.1002/ece3.1878

Loeuille B, Semir J, Pirani JR (2019) A synopsis of Lychnophorinae (Asteraceae: Vernonieae). Phytotaxa 398:1–139. https://doi.org/10.11646/phytotaxa.398.1.1

Loram-Lourenço L, Farnese F dos S, Sousa LF de, et al (2020) A Structure Shaped by Fire, but Also Water: Ecological Consequences of the Variability in Bark Properties Across 31 Species From the Brazilian Cerrado. Frontiers in Plant Science 10:1718. https://doi.org/10.3389/fpls.2019.01718

Macedo GF, Almeida-Bezerra JW, Silva VB da, et al (2020) Eremanthus arboreus (Gardner) MacLeish (Candeeiro): natural source of α-Bisabolol. Research, Society and Development 9:e9599109270. https://doi.org/10.33448/rsd-v9i10.9270

Machado NA de M, Leite MGP, Figueiredo MA, Kozovits AR (2013) Growing Eremanthus erythropappus in crushed laterite: A promising alternative to topsoil for bauxite-mine revegetation. Journal of Environmental Management 129:149–156. https://doi.org/10.1016/j.jenvman.2013.07.006

MacLeish NFF (1987) Revision of Eremanthus (Compositae: Vernonieae). Annals of the Missouri Botanical Garden 74:265–290. https://doi.org/10.2307/2399398

Marcer A, Sáez L, Molowny-Horas R, et al (2013) Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. Biological Conservation 166:221–230. https://doi.org/10.1016/j.biocon.2013.07.001

Marco P de, Villén S, Mendes P, et al (2018) Vulnerability of Cerrado threatened mammals: an integrative landscape and climate modeling approach. Biodiversity and Conservation 29:1637–1658. https://doi.org/10.1007/s10531-018-1615-x

Martinelli G, Moraes MA (2013) Livro vermelho da flora do Brasil, 1º ed. Centro Nacional de Conservação da Flora, Rio de Janeiro

Mcdonald RI, Forman RTT, Kareiva P, et al (2009) Urban effects, distance, and protected areas in an urbanizing world. Landscape and Urban Planning 93:63–75. https://doi.org/10.1016/j.landurbplan.2009.06.002

Mcdonald RI, Kareiva P, Forman RTT (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695–1703. https://doi.org/10.1016/j.biocon.2008.04.025

Moat J, Gole TW, Davis AP (2019) Least concern to endangered: Applying climate change projections profoundly influences the extinction risk assessment for wild Arabica coffee. Global Change Biology 25:390–403. https://doi.org/10.1111/gcb.14341

Morrone JJ, Escalante T, Rodríguez-Tapia G, et al (2022) Biogeographic regionalization of the Neotropical region: New map and shapefile. Anais da Academia Brasileira de Ciências 94:e20211167. https://doi.org/10.1590/0001-3765202220211167

Mucina L, Wardell-Johnson GW (2011) Landscape age and soil fertility, climatic stability, and fire regime predictability: Beyond the OCBIL framework. Plant and Soil 341:1–23. https://doi.org/10.1007/s11104-011-0734-x

Ncube B, Finnie JF, van Staden J (2011) Seasonal variation in antimicrobial and phytochemical properties of frequently used medicinal bulbous plants from South Africa. South African Journal of Botany 77:387–396. https://doi.org/10.1016/j.sajb.2010.10.004

Neves DM, Dexter KG, Pennington RT, et al (2018) Lack of floristic identity in campos rupestres — A hyperdiverse mosaic of rocky montane savannas in South America. Flora 238:24–31. https://doi.org/10.1016/j.flora.2017.03.011

Oliveira U, Soares-Filho BS, Paglia AP, et al (2017) Biodiversity conservation gaps in the Brazilian protected areas. Scientific Reports 7:9141. https://doi.org/10.1038/s41598-017-08707-2

Ortega-Huerta MA, Peterson AT (2004) Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico. Diversity and Distributions 10:39–54. https://doi.org/10.1111/j.1472-4642.2004.00051.x

Pádua JAR de, Brandão MM, de Carvalho D (2016) Spatial genetic structure in natural populations of the overexploited tree Eremanthus erythropappus (DC.) macleish (Asteraceae). Biochemical Systematics and Ecology 66:307–311. https://doi.org/10.1016/j.bse.2016.04.015

Pádua JAR de, Rocha LF, Brandão MM, et al (2021) Title: priority areas for genetic conservation of Eremanthus erythropappus (DC.) MacLeish in Brazil. Genetic Resources and Crop Evolution. https://doi.org/10.1007/s10722-021-01144-1

Panter CT, Clegg RL, Moat J, et al (2020) To clean or not to clean: Cleaning open-source data improves extinction risk assessments for threatened plant species. Conservation Science and Practice 2:e311. https://doi.org/10.1111/csp2.311

Pena JC de C, Goulart F, Fernandes GW, et al (2017) Impacts of mining activities on the potential geographic distribution of eastern Brazil mountaintop endemic species. Perspectives in Ecology and Conservation 15:172–178. https://doi.org/10.1016/j.pecon.2017.07.005

Peterson AT (2011) Ecological niche conservatism: A time-structured review of evidence. Journal of Biogeography 38:817–827. https://doi.org/10.1111/j.1365-2699.2010.02456.x

Peterson AT, Papes M, Reynolds MG, et al (2006) Native-Range Ecology and Invasive Potential of Cricetomys in North America. Journal of Mammalogy 87:427–432. https://doi.org/10.1644/05-mamm-a-133r3.1

Peterson AT, Robins CR (2003) Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation. Conservation Biology 17:1161–1165. https://doi.org/10.1046/j.1523-1739.2003.02206.x

Peterson AT, Soberón J, Pearson RG, et al (2011) Ecological Niches and Geographic Distributions. Princeton University Press, Princeton

Peterson ML, Doak DF, Morris WF (2019) Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. Global Change Biology 25:775–793. https://doi.org/10.1111/gcb.14562

Pivello VR, Shida CN, Meirelles ST (1999) Alien grasses in Brazilian savannas: a threat to the biodiversity. Biodiversity and Conservation 8:1281–1294. https://doi.org/10.1023/A:1008933305857

QGIS Development Team (2020) QGIS Geographic Information System [Computer software]

R Core Team (2020) A language and environment for statistical computing [Computer software]

Rai LK, Prasad P, Sharma E (2000) Conservation threats to some important medicinal plants of the Sikkim Himalaya. Biological Conservation 93:27–33. https://doi.org/10.1016/S0006-3207(99)00116-0

Rapini A, Bitencourt C, Luebert F, Cardoso D (2021) An escape-to-radiate model for explaining the high plant diversity and endemism in campos rupestres†. Biological Journal of the Linnean Society 133:481–498. https://doi.org/10.1093/biolinnean/blaa179

Rapini A, Ribeiro PL, Lambert S, Pirani JR (2008) A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4:16–24

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. Annals of Botany 80:223–230. https://doi.org/10.1006/anbo.1997.0469

Razgour O, Forester B, Taggart JB, et al (2019) Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proc Natl Acad Sci U S A 116:10418–10423. https://doi.org/10.1073/pnas.1820663116

Rissi MN, Baeza MJ, Gorgone-Barbosa E, et al (2017) Does season affect fire behaviour in the Cerrado? International Journal of Wildland Fire 26:427–433. https://doi.org/10.1071/WF14210

Rocha LF, Paula NR de, Carvalho D de (2020a) Fine-scale analysis reveals a potential influence of forest management on the spatial genetic structure of Eremanthus erythropappus. Journal of Forestry Research. https://doi.org/10.1007/s11676-020-01204-9

Rocha LF, Paula NR, Nazareno AG, Carvalho D de (2020b) Development and characterization of nuclear microsatellite markers for Eremanthus erythropappus and their transferability across related species. Biological Research 53:30. https://doi.org/10.1186/s40659-020-00298-z

Rosser AM, Mainka SA (2002) Overexploitation and Species Extinctions. Conservation Biology 16:584–586. https://doi.org/10.1046/j.1523-1739.2002.01635.x

RStudio Team (2020) RStudio: Integrated Development Environment for R [Computer software]

Sánchez-Tapia A, de Siqueira MF, Lima RO, et al (2018) Model-R: A framework for scalable and reproducible ecological niche modeling. Communications in Computer and Information Science 796:218–232. https://doi.org/10.1007/978-3-319-73353-1_15

Sangermano F, Eastman JR (2012) A GIS framework for the refinement of species geographic ranges. International Journal of Geographical Information Science 26:39–55. https://doi.org/10.1080/13658816.2011.567987

Scarano FR, Ceotto P, Medeiros R, Mittermeier RA (2014) O bioma Cerrado: conservação e ameaças. In: Martinelli G, Messina T, Santos Filho L (eds) Livro Vermelho da flora do Brasil – Plantas raras do Cerrado, 1º Ed. Centro Nacional de Conservação da Flora, Rio de Janeiro, pp 21–24

Scolforo JR, Oliveira AD de, Davide AC, Camolesi JF (2002) Manejo sustentado das candeias Eremanthus erythropappus (DC.) McLeisch e Eremanthus incanus (Less.) Less. Lavras, UFLA

Scott JM, Davis F, Csuti B, et al (1993) Gap Analysis: A Geographic Approach to Protection of Biological Diversity. Wildlife Monographs 123:3–41

Silva AC, Horàk-Terra I, Barral UM, et al (2020) Altitude, vegetation, paleoclimate, and radiocarbon age of the basal layer of peatlands of the Serra do Espinhaço Meridional, Brazil. Journal of South American Earth Sciences 103:102728. https://doi.org/10.1016/j.jsames.2020.102728

Silveira FAO, Dayrell RLC, Fiorini CF, et al (2020) Diversification in Ancient and Nutrient-Poor Neotropical Ecosystems: How Geological and Climatic Buffering Shaped Plant Diversity in Some of the World’s Neglected Hotspots. In: Rull V, Carnaval AC (eds) Neotropical Diversification: Patterns and Processes. Springer, Cham

Silveira FAO, Fiedler PL, Hopper SD (2021) OCBIL theory: a new science for old ecosystems. Biological Journal of the Linnean Society 133:251–265. https://doi.org/10.1093/biolinnean/blab038

Silveira FAO, Negreiros D, Barbosa NPU, et al (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant and Soil 403:129–152. https://doi.org/10.1007/s11104-015-2637-8

Simon MF, Grether R, de Queiroz LP, et al (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences 106:20359–20364. https://doi.org/10.1073/pnas.0903410106

Simon MF, Pennington T (2012) Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. International Journal of Plant Sciences 173:711–723. https://doi.org/10.1086/665973

Sinclair SJ, White MD, Newell GR (2010) How Useful Are Species Distribution Models for Managing Biodiversity under Future Climates? Ecology and Society 15:art8. https://doi.org/10.5751/ES-03089-150108

Siqueira MF de, Durigan G (2007) Modelagem da distribuição geográfica de espécies lenhosas de cerrado no Estado de São Paulo. Revista Brasileira de Botânica 30:233–243. https://doi.org/10.1590/s0100-84042007000200008

Souza-Neto AC, Cianciaruso M v., Collevatti RG (2016) Habitat shifts shaping the diversity of a biodiversity hotspot through time: Insights from the phylogenetic structure of Caesalpinioideae in the Brazilian Cerrado. Journal of Biogeography 43:340–350. https://doi.org/10.1111/jbi.12634

Steig EJ (1999) Mid-Holocene climate change. Science (1979) 286:1485–1487. https://doi.org/10.1126/science.286.5444.1485

Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. Ecological Modelling 148:1–13. https://doi.org/10.1016/S0304-3800(01)00388-X

Strassburg BBN, Brooks T, Feltran-Barbieri R, et al (2017) Moment of truth for the Cerrado hotspot. Nature Ecology and Evolution 1:0099. https://doi.org/10.1038/s41559-017-0099

Syfert MM, Joppa L, Smith MJ, et al (2014) Using species distribution models to inform IUCN Red List assessments. Biological Conservation 177:174–184. https://doi.org/10.1016/j.biocon.2014.06.012

Terra M de CNS, dos Santos RM, Fontes MAL, et al (2017) Tree dominance and diversity in Minas Gerais, Brazil. Biodiversity and Conservation 26:2133–2153. https://doi.org/10.1007/s10531-017-1349-1

Thuiller W, Albert C, Araújo MB, et al (2008) Predicting global change impacts on plant species’ distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9:137–152. https://doi.org/10.1016/j.ppees.2007.09.004

Valencia JB, Mesa J, León JG, et al (2020) Climate Vulnerability Assessment of the Espeletia Complex on Páramo Sky Islands in the Northern Andes. Frontiers in Ecology and Evolution 8:565708. https://doi.org/10.3389/fevo.2020.565708

Velazco SJE, Villalobos F, Galvão F, de Marco Júnior P (2019) A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. Diversity and Distributions 25:660–673. https://doi.org/10.1111/ddi.12886

Verma P, Mathur AK, Jain SP, Mathur A (2012) In vitro conservation of twenty-three overexploited medicinal plants belonging to the indian sub continent. The Scientific World Journal 2012:. https://doi.org/10.1100/2012/929650

Vidal J de D, de Souza AP, Koch I (2019) Impacts of landscape composition, marginality of distribution, soil fertility and climatic stability on the patterns of woody plant endemism in the Cerrado. Global Ecology and Biogeography 28:904–916. https://doi.org/10.1111/geb.12901

Visconti P, Bakkenes M, Baisero D, et al (2016) Projecting Global Biodiversity Indicators under Future Development Scenarios. Conservation Letters 9:5–13. https://doi.org/10.1111/conl.12159

Wanner H, Beer J, Bütikofer J, et al (2008) Mid- to Late Holocene climate change: an overview. Quaternary Science Reviews 27:1791–1828. https://doi.org/10.1016/j.quascirev.2008.06.013

Williams SJ, Jones JPG, Annewandter R, Gibbons JM (2014) Cultivation can increase harvesting pressure on overexploited plant populations. Ecological Applications 24:2050–2062. https://doi.org/10.1890/13-2264.1

Wisz MS, Hijmans RJ, Li J, et al (2008) Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Figures captions

Fig. 1 (**a**) Large deforested area where a population of *E. rondoniensis* was present at least until 2004; (**b**) *E. capitatus*; (**c**) *E. incanus*; (**d**) *E. elaeagnus*; (**e**) *E. erythropappus* wood being used as bridge structure.

Fig. 2 *E. erythropappus* Mid-Holocene suitability areas. Gray-scale areas show the environmental suitability of the Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins.

Fig. 3 *E. erythropappus* present time suitability areas and Gap Analysis results. The grey-scale areas show the environmental suitability of Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. The line involving the environmental suitability area represents the modelling Minimum Convex Polygon (MCP) and the dashed line corresponds to records MCP. The areas suitable for species establishment are in blue and Protected Areas (PAs) are in red. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins.

Fig. 4 *E. erythropappus* future (2070 – RCP 8.5) suitability areas and Gap Analysis results. The grey-scale areas show the environmental suitability of Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. The line involving the environmental suitability area represents the modelling Minimum Convex Polygon (MCP) and the dashed line corresponds to records MCP. The areas suitable for species establishment are in blue and Protected Areas (PAs) are in red. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins.

Table 1 Percentage values found for records in protected areas (Records PAs), protected areas in suitability area for present and future models (Present PAs and Future PAs) and suitability area loss estimated for total area and protected areas (TAs Loss and PAs Loss) related to SDM models. PA = Protected area; TA = Total area.

Species	Records PAs	Present PAs	Future PAs	TAs Loss	PAs Loss
E. capitatus	21%	14%	28%	89%	79%
E. cinctus	8%	15%	60%	96%	86%
E. crotonoides	26%	20%	61%	82%	48%
E. elaeagnus	35%	19%	47%	75%	40%
E. erythropappus	28%	27%	68%	74%	38%
E. glomerulatus	41%	16%	49%	91%	74%
E. goyazensis	37%	17%	42%	92%	81%
E. incanus	26%	18%	54%	86%	60%
E. mattogrossensis	22%	12%	41%	97%	92%
E. mollis	36%	17%	56%	92%	77%
E. polycephalus	29%	12%	38%	83%	51%
E. reticulatus	25%	22%	37%	53%	21%
E. rondoniensis	26%	12%	25%	51%	2%
E. syncephalus	33%	26%	47%	68%	43%
E. uniflorus	72%	22%	34%	95%	93%

Table 2 Extent of Occurrence and Area of Occupancy of the records in km^2 (EOOr and AOOr), proposed IUCN categories (IUCN Category) and projected loss percentages of the Extent of Occurrence and Area of Occupancy, considering the total area (EOOtl and AOOtl) and the records Minimum Convex Polygon (EOOhl and AOOhl). EOO = Extent of Occurrence; AOO = Area of Occupancy; MCP = Minimum Convex Polygon, VU = Vulnerable; EN = Endangered; h = convex hull (MCP); l = loss percentage; r = records; t = total area.

Species	EOOr	AOOr	IUCN Category	EOOtl	AOOtl	EOOhl	AOOhl
E. capitatus	885,507 km^2	616 km^2	VU	30%	89%	65%	94%
E. cinctus	360,580 km^2	48 km^2	EN	94%	92%	100%	100%
E. crotonoides	519,587 km^2	516 km^2	VU	75%	77%	75%	90%
E. elaeagnus	125,365 km^2	204 km^2	EN	56%	85%	77%	90%
E. erythropappus	690,176 km^2	584 km^2	VU	50%	81%	62%	85%
E. glomerulatus	777,541 km^2	612 km^2	VU	59%	87%	66%	91%
E. goyazensis	357,086 km^2	296 km^2	EN	74%	80%	96%	96%
E. incanus	439,893 km^2	508 km^2	VU	57%	90%	66%	93%
E. mattogrossensis	1,692,804 km^2	312 km^2	EN	49%	90%	69%	95%
E. mollis	202,975 km^2	132 km^2	EN	81%	85%	98%	98%
E. polycephalus	92,945 km^2	140 km^2	EN	48%	88%	51%	92%
E. reticulatus	104,652 km^2	64 km^2	EN	35%	65%	34%	53%
E. rondoniensis	90,008 km^2	72 km^2	EN	61%	59%	65%	79%
E. syncephalus	168,166 km^2	124 km^2	EN	35%	81%	39%	87%
E. uniflorus	32,071 km^2	40 km^2	EN	98%	91%	100%	100%

Figure 1

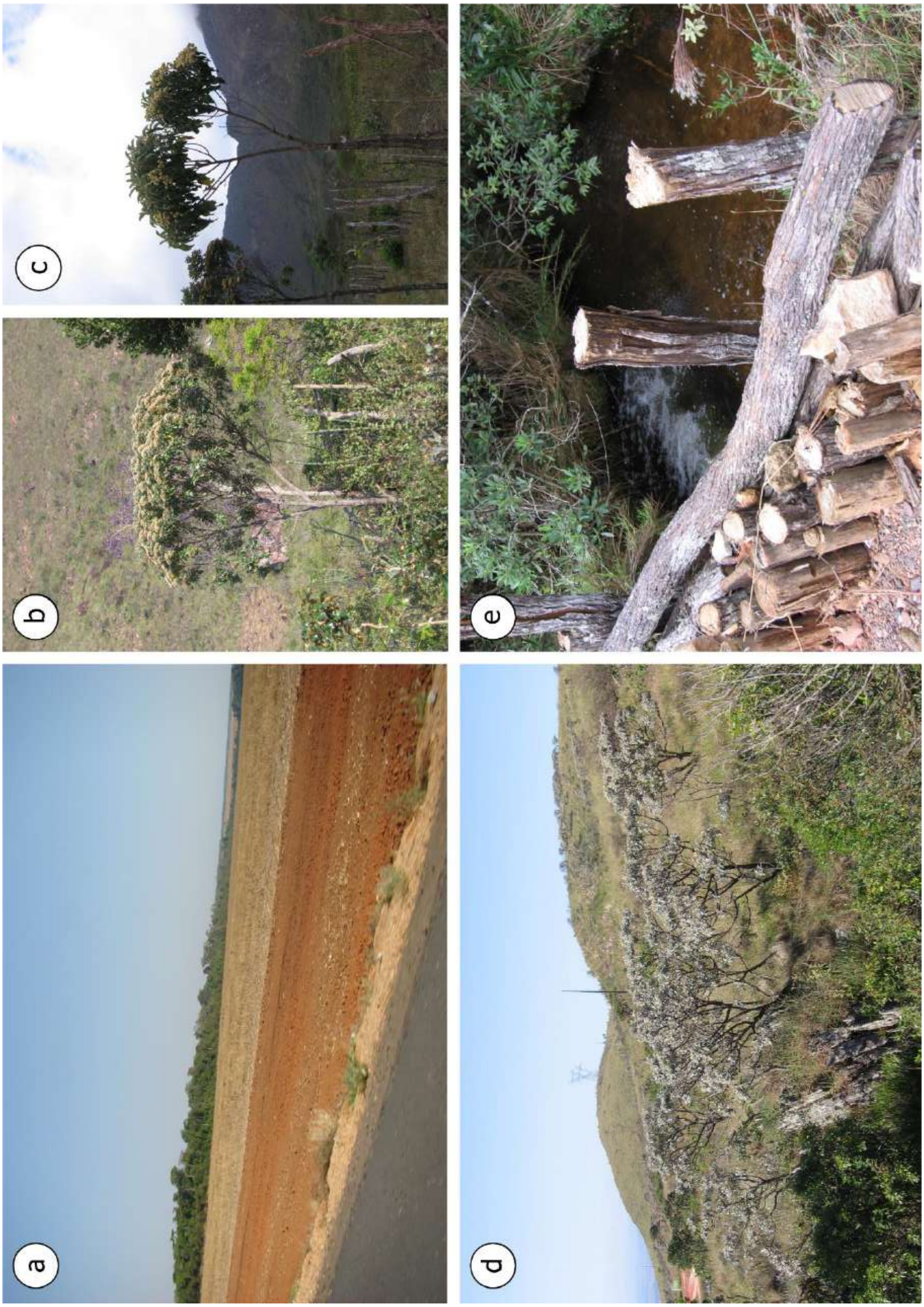
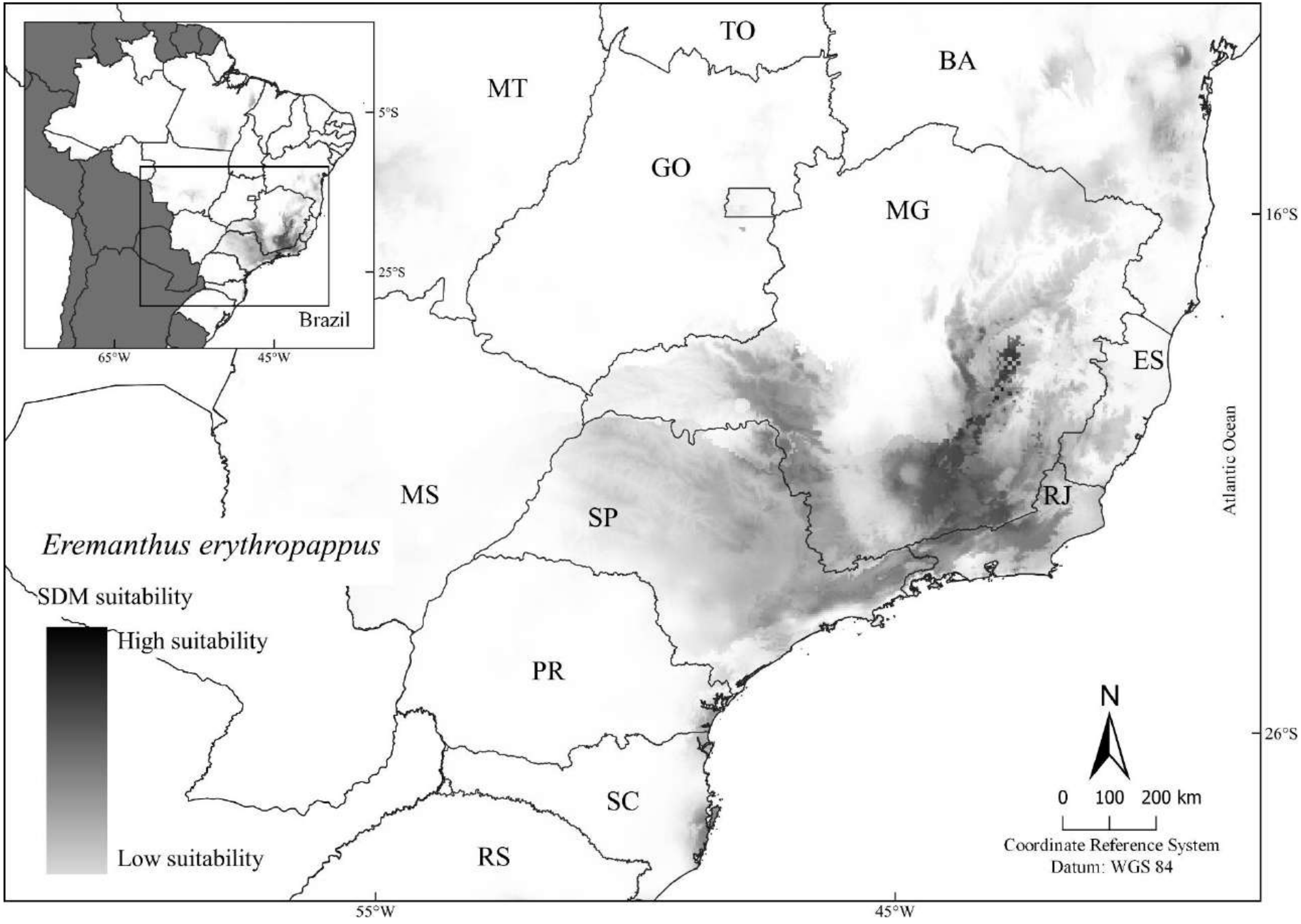


Figure 2


Eremanthus erythropappus
SDM suitability
High suitability
Low suitability
MT
TO
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SC
RS
Atlantic Ocean
N
0 100 200 km
Coordinate Reference System
Datum: WGS 84
16°S
26°S
55°W
45°W
Brazil
5°S
25°S
65°W
45°W

Figure 3

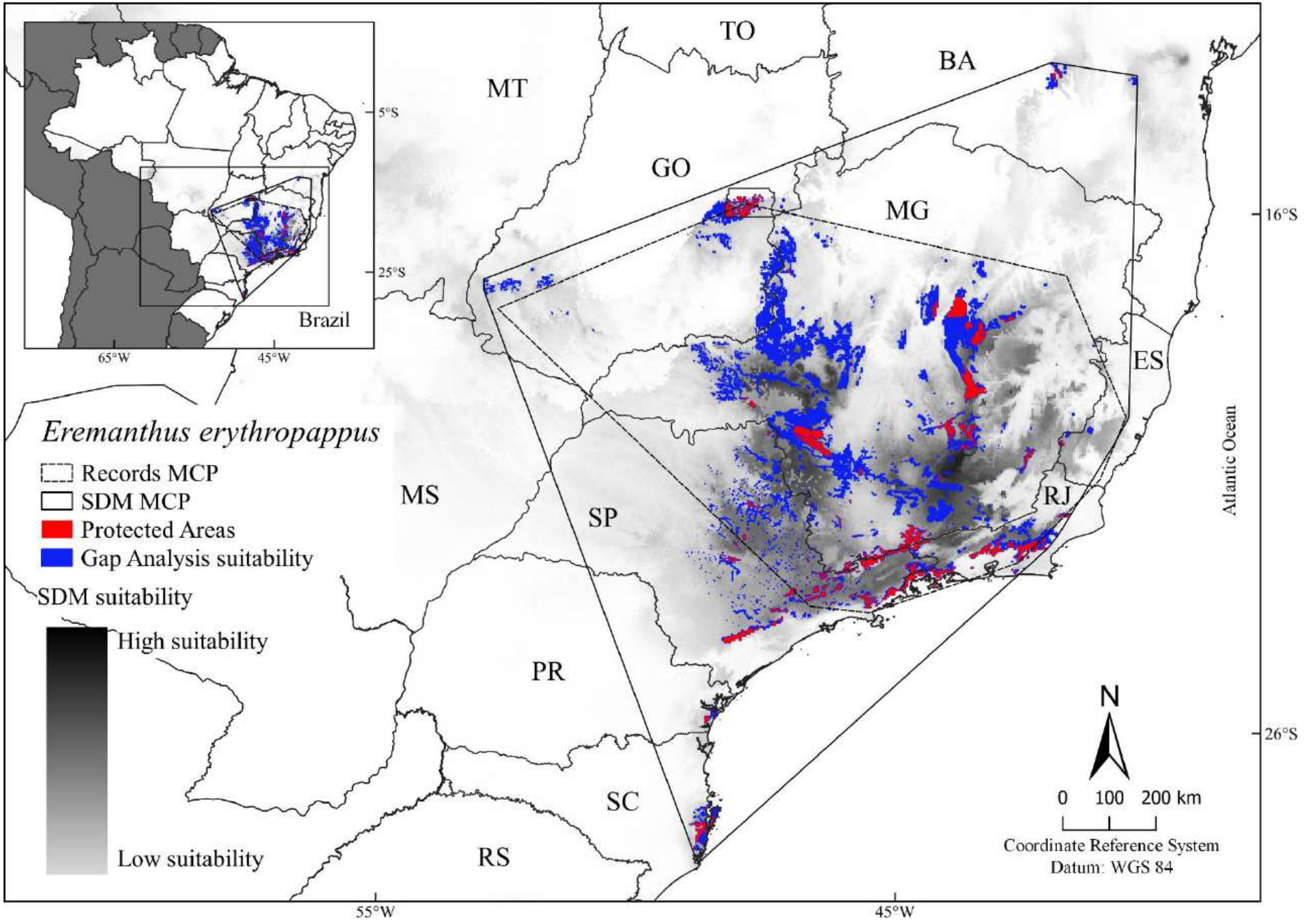
Eremanthus erythropappus
Records MCP
SDM MCP
🟥 Protected Areas
🟦 Gap Analysis suitability
SDM suitability
High suitability
Low suitability
Brazil
5°S
25°S
65°W
45°W
TO
BA
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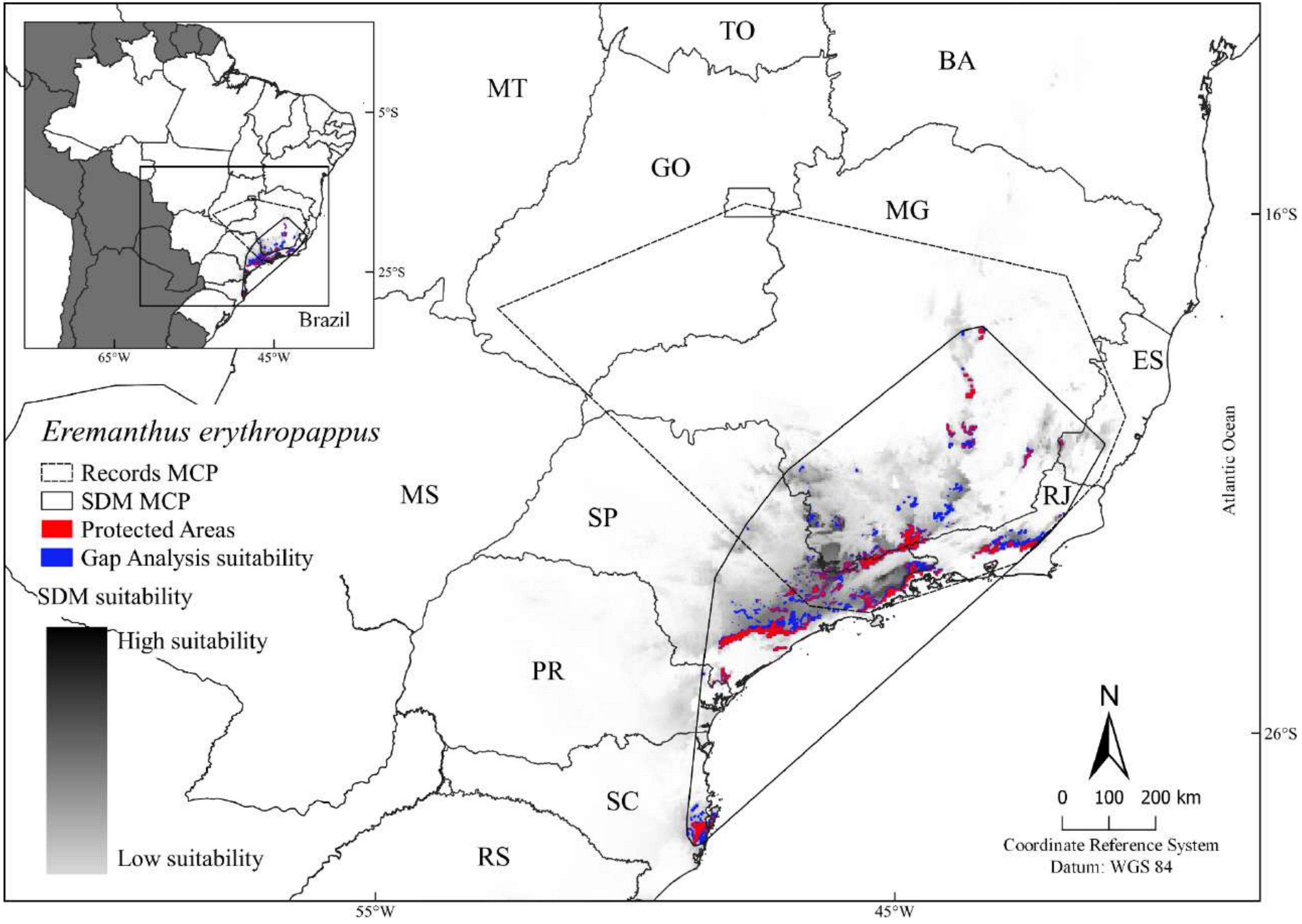
Figure 4


Eremanthus erythropappus
Records MCP
SDM MCP
Protected Areas
Gap Analysis suitability
SDM suitability
High suitability
Low suitability
Brazil
5°S
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MT
TO
BA
GO
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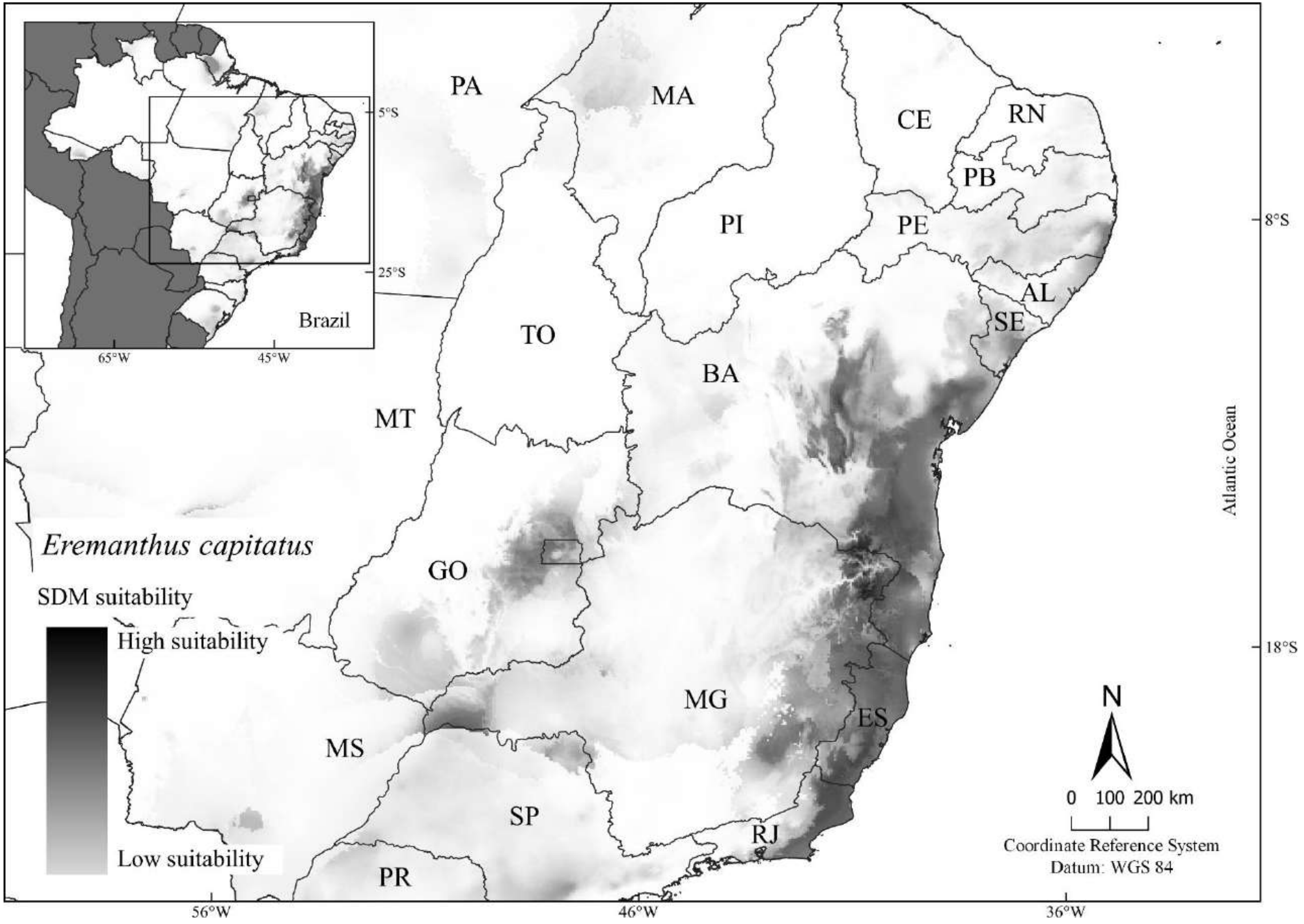
Online Resource 1



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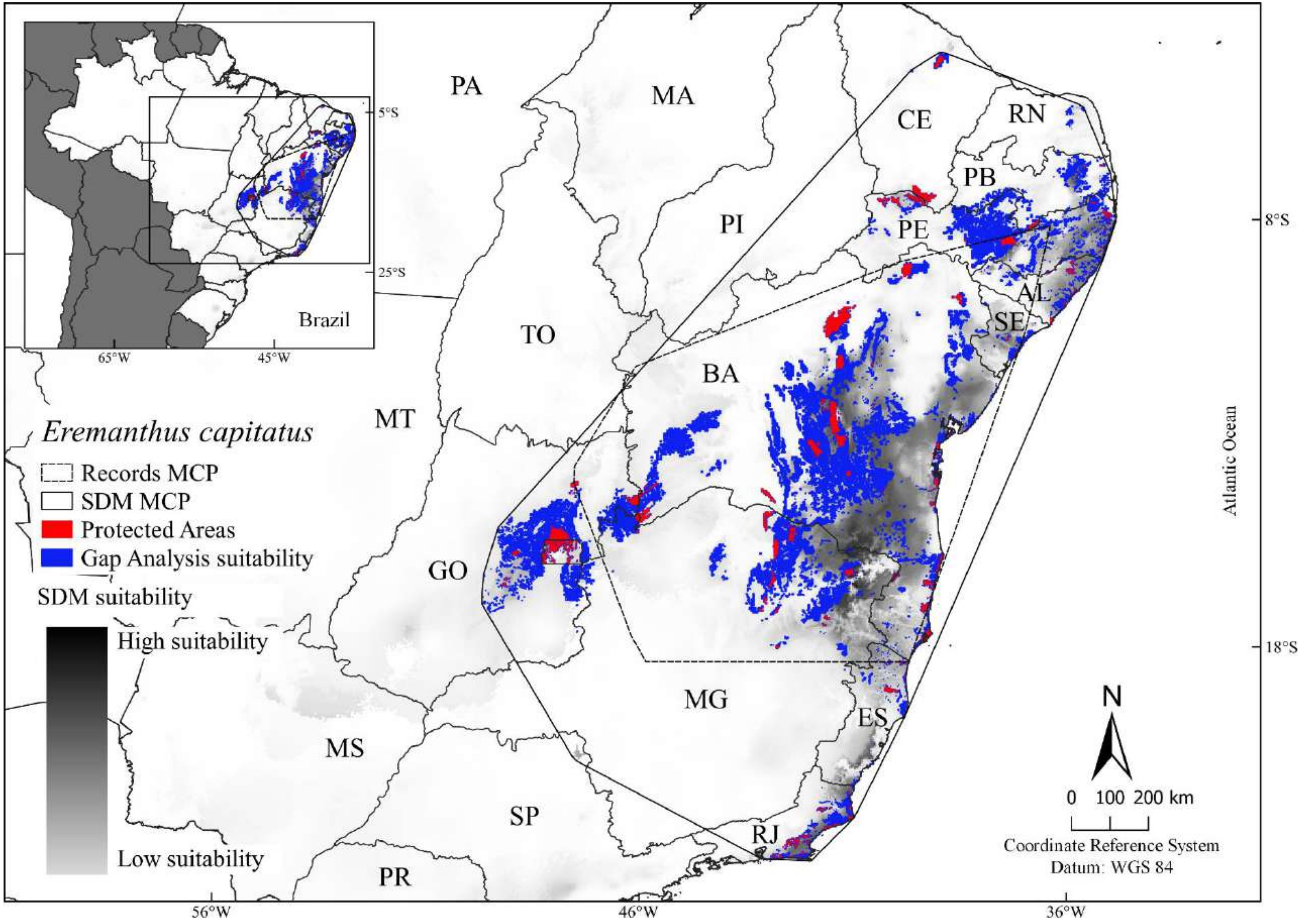

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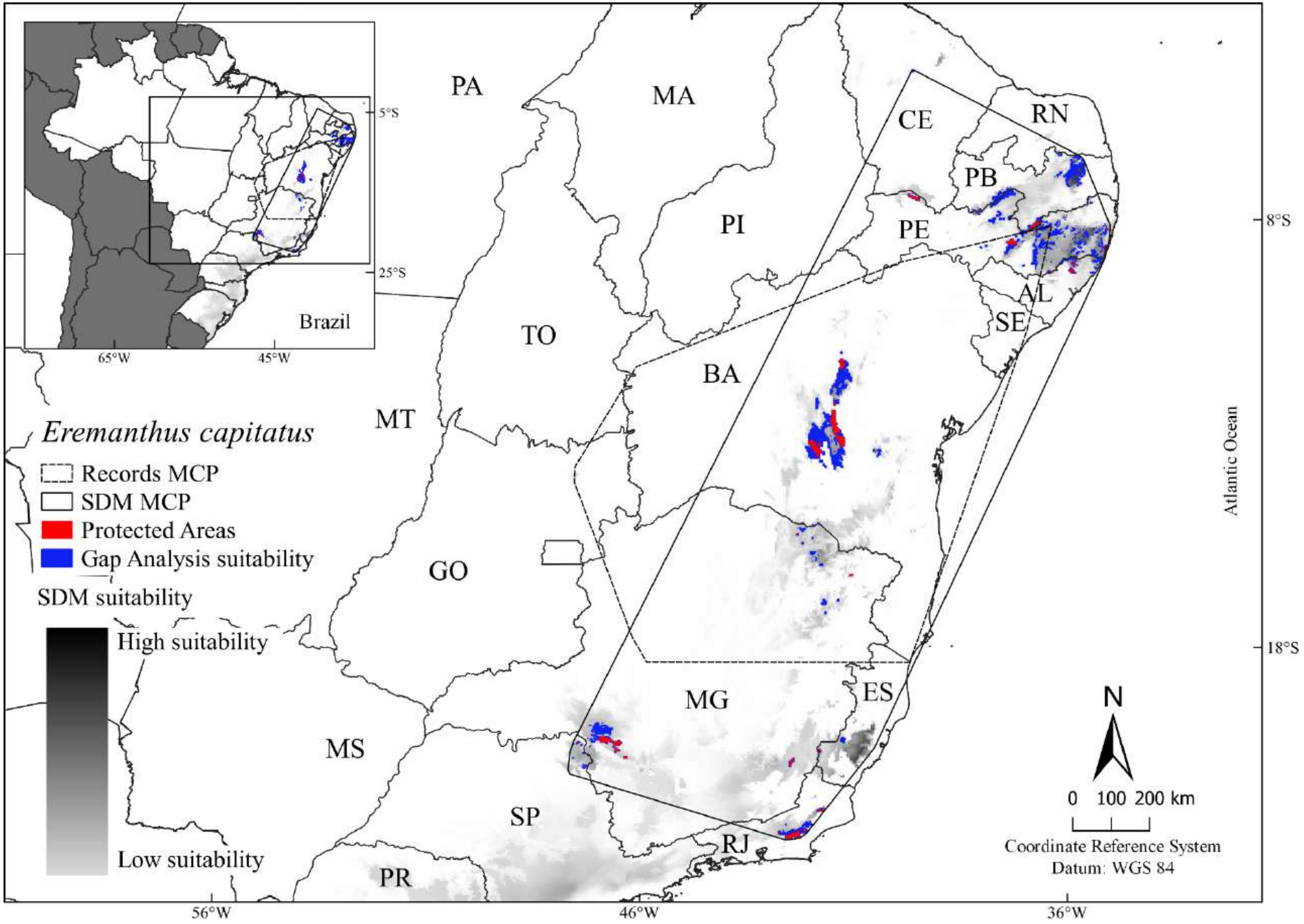

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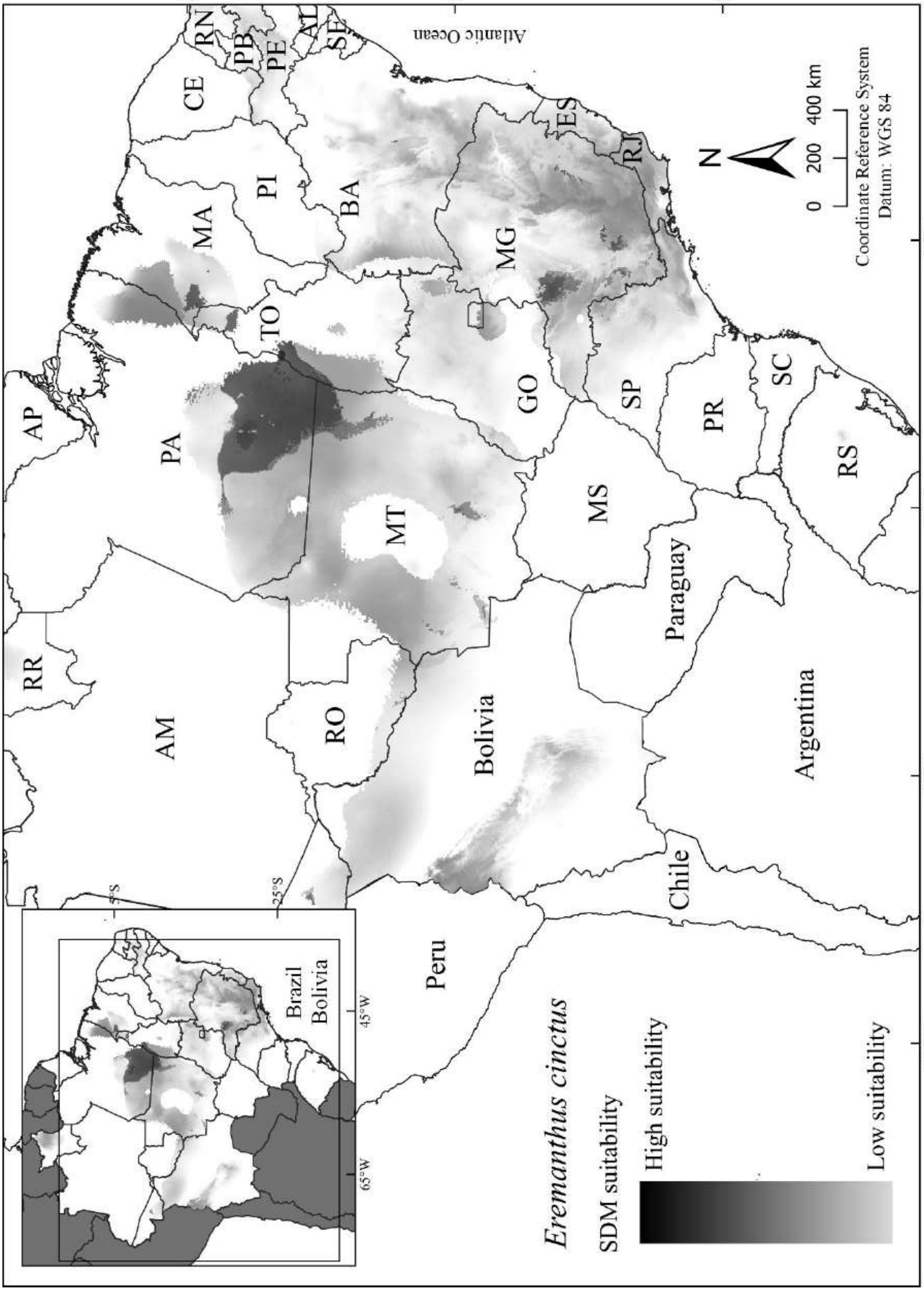

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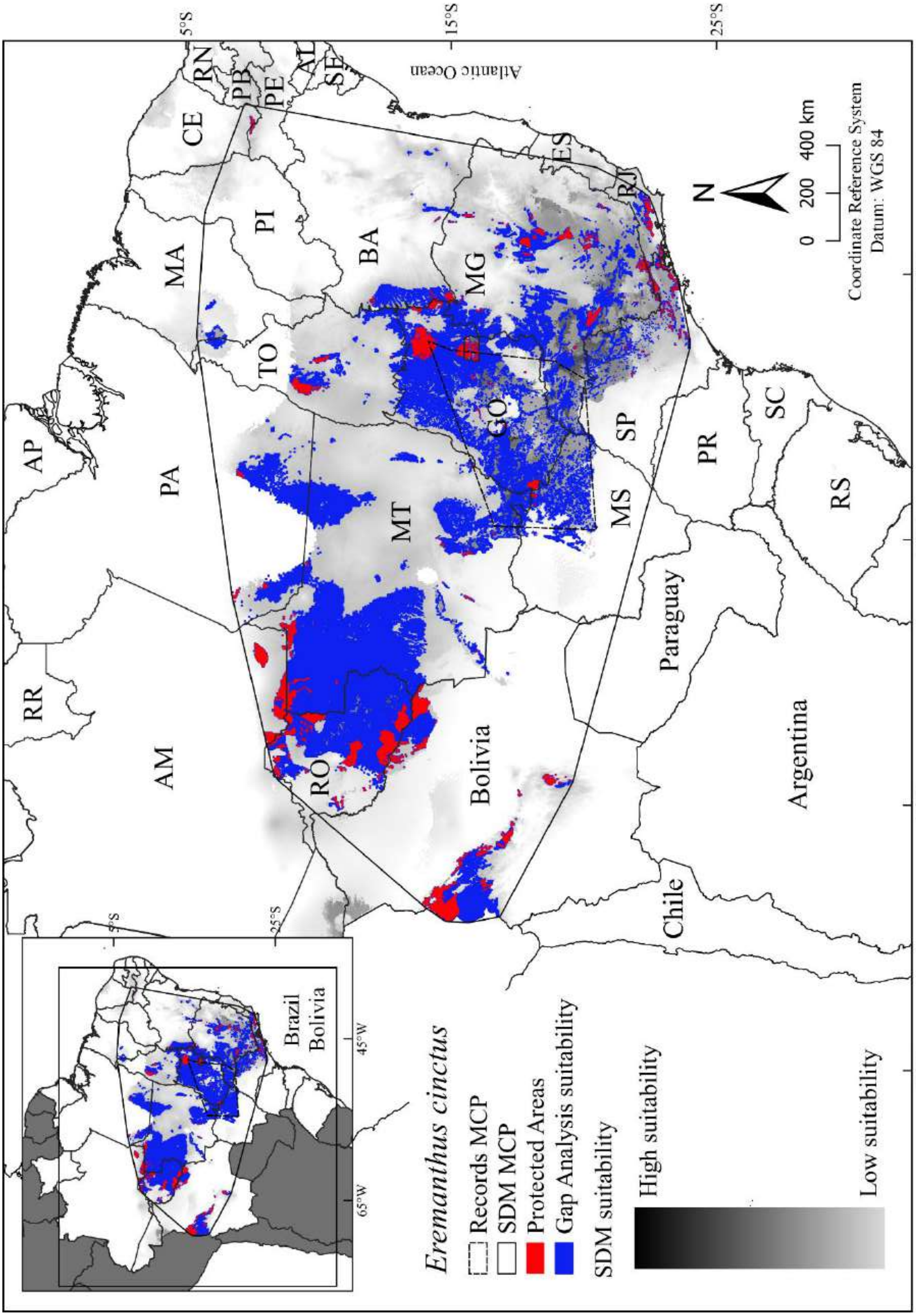

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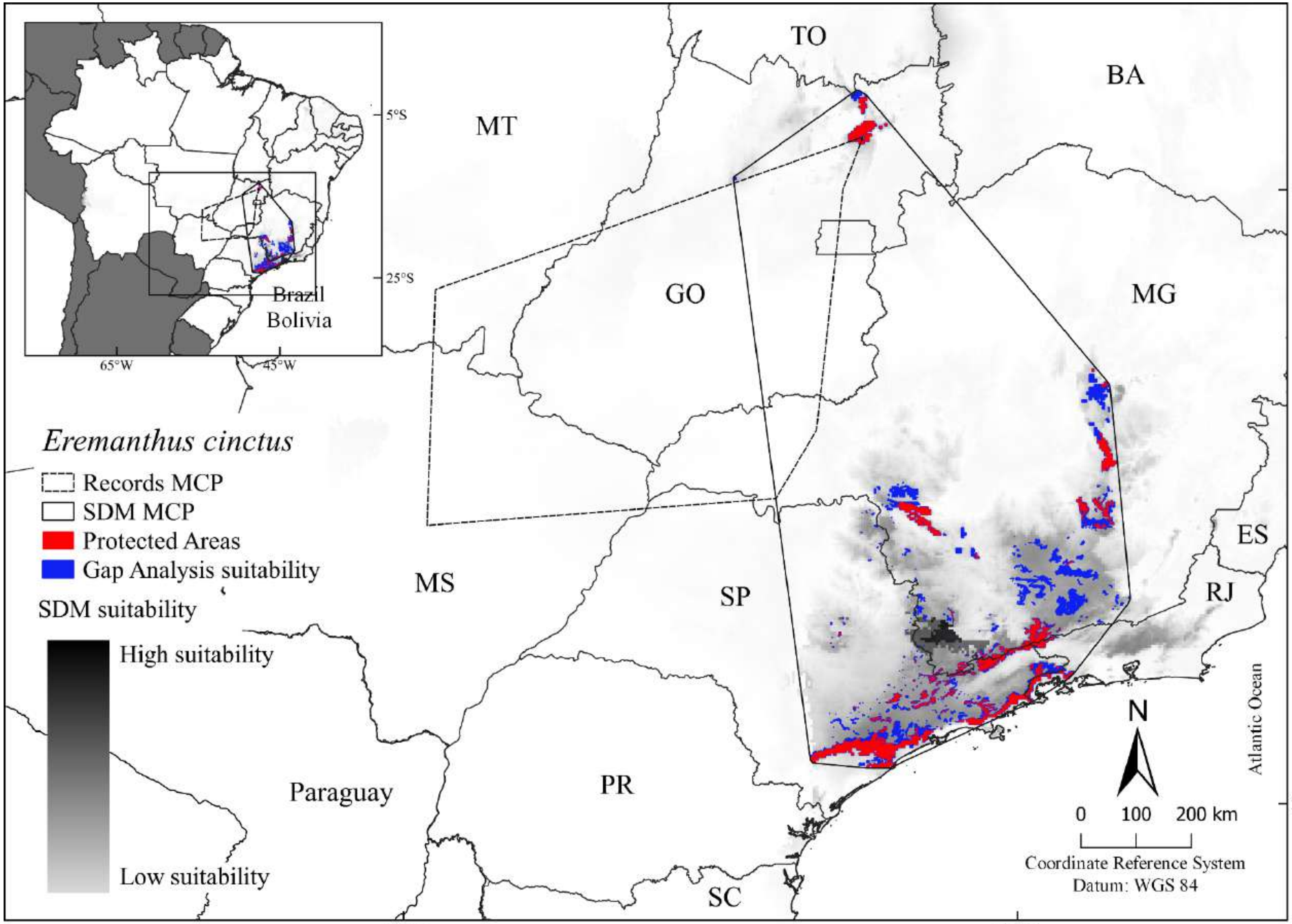

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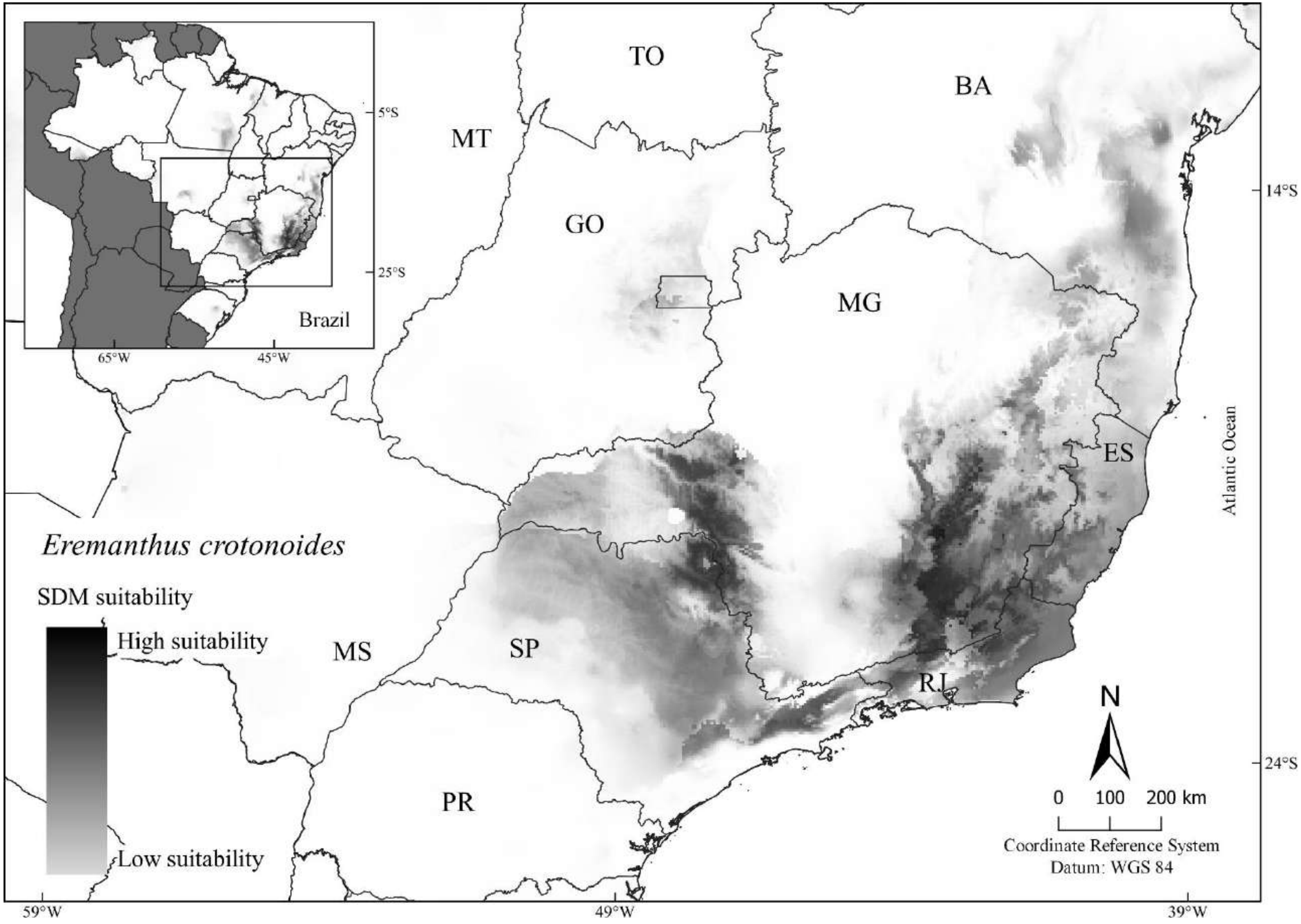

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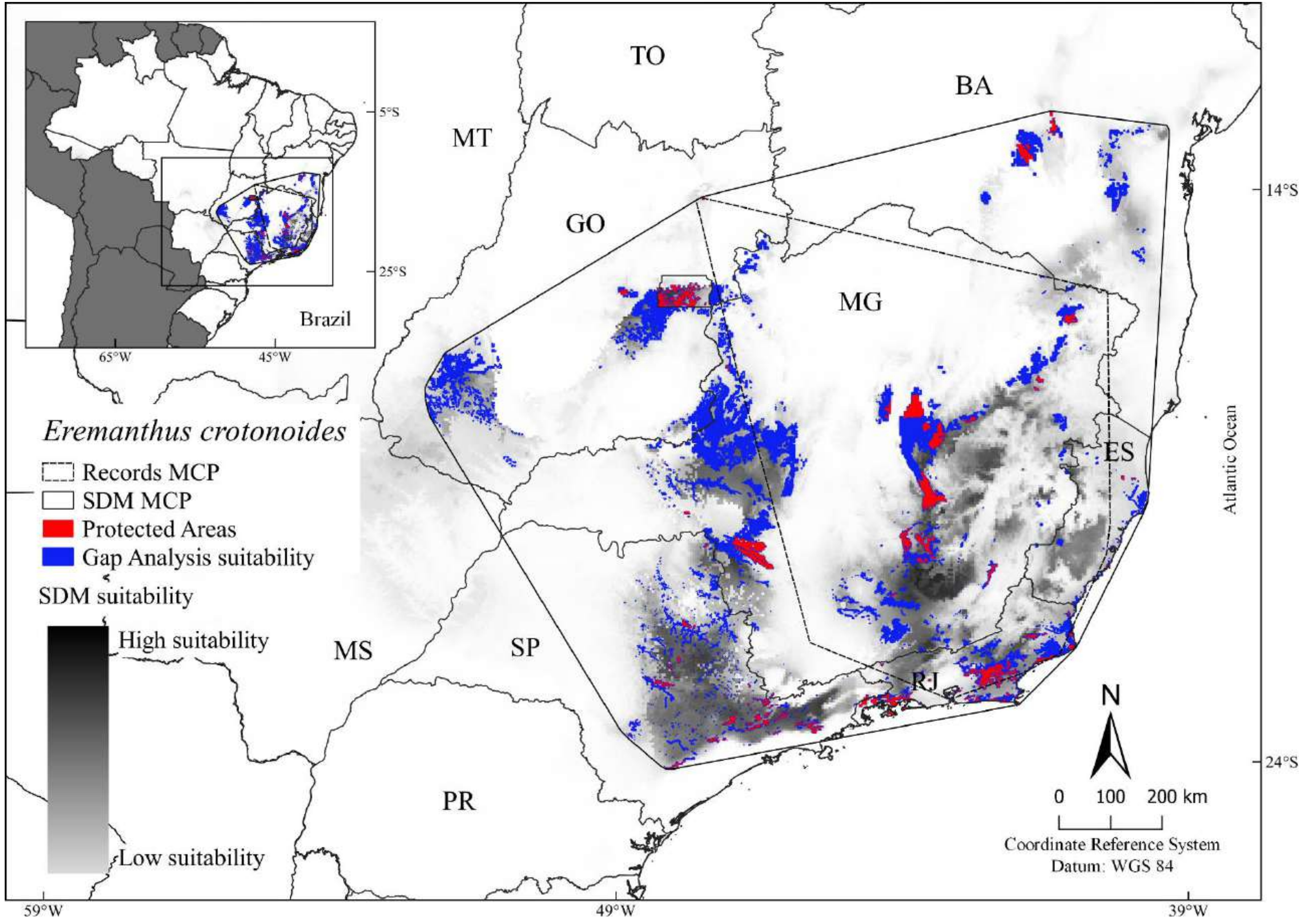

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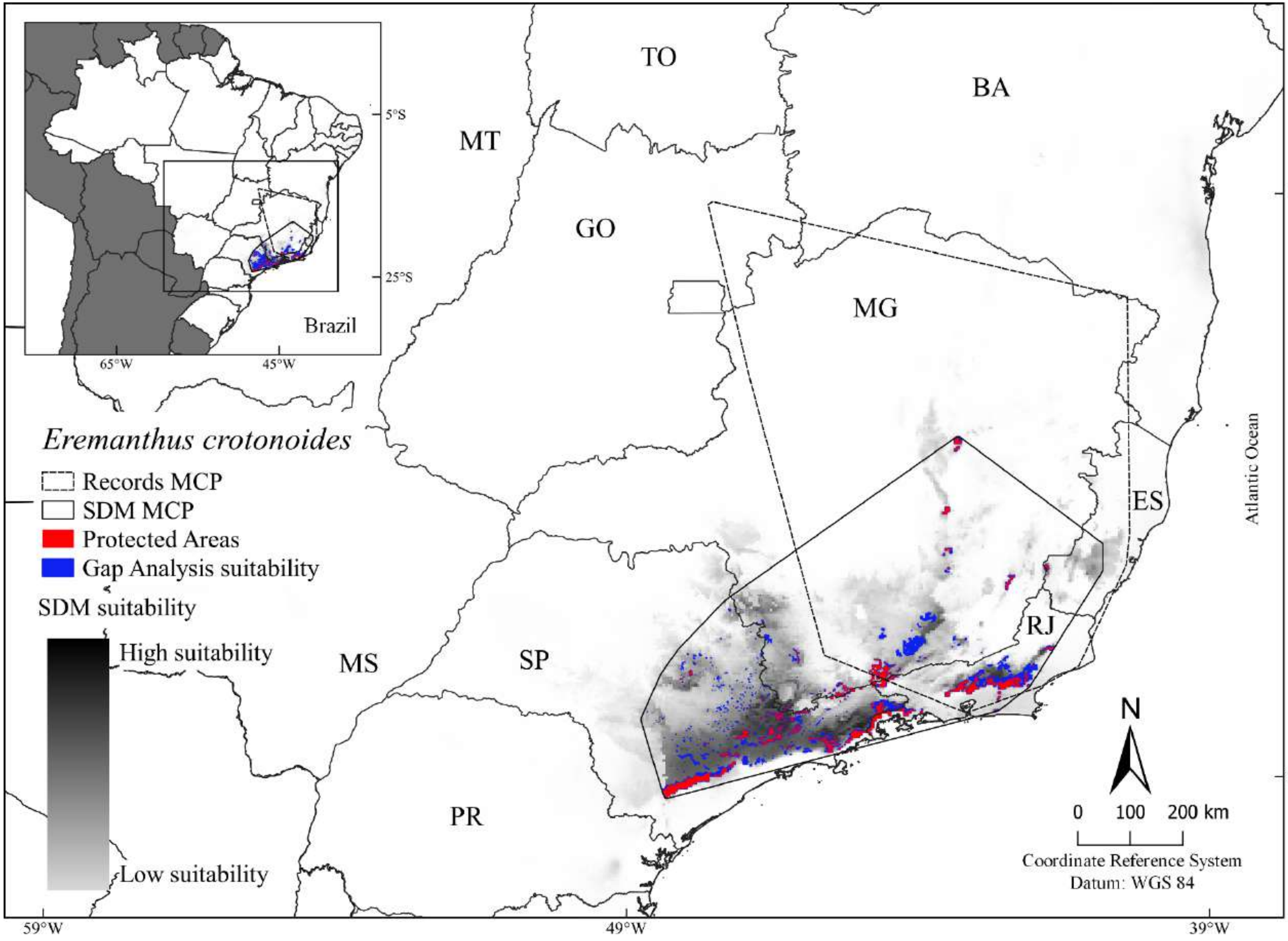

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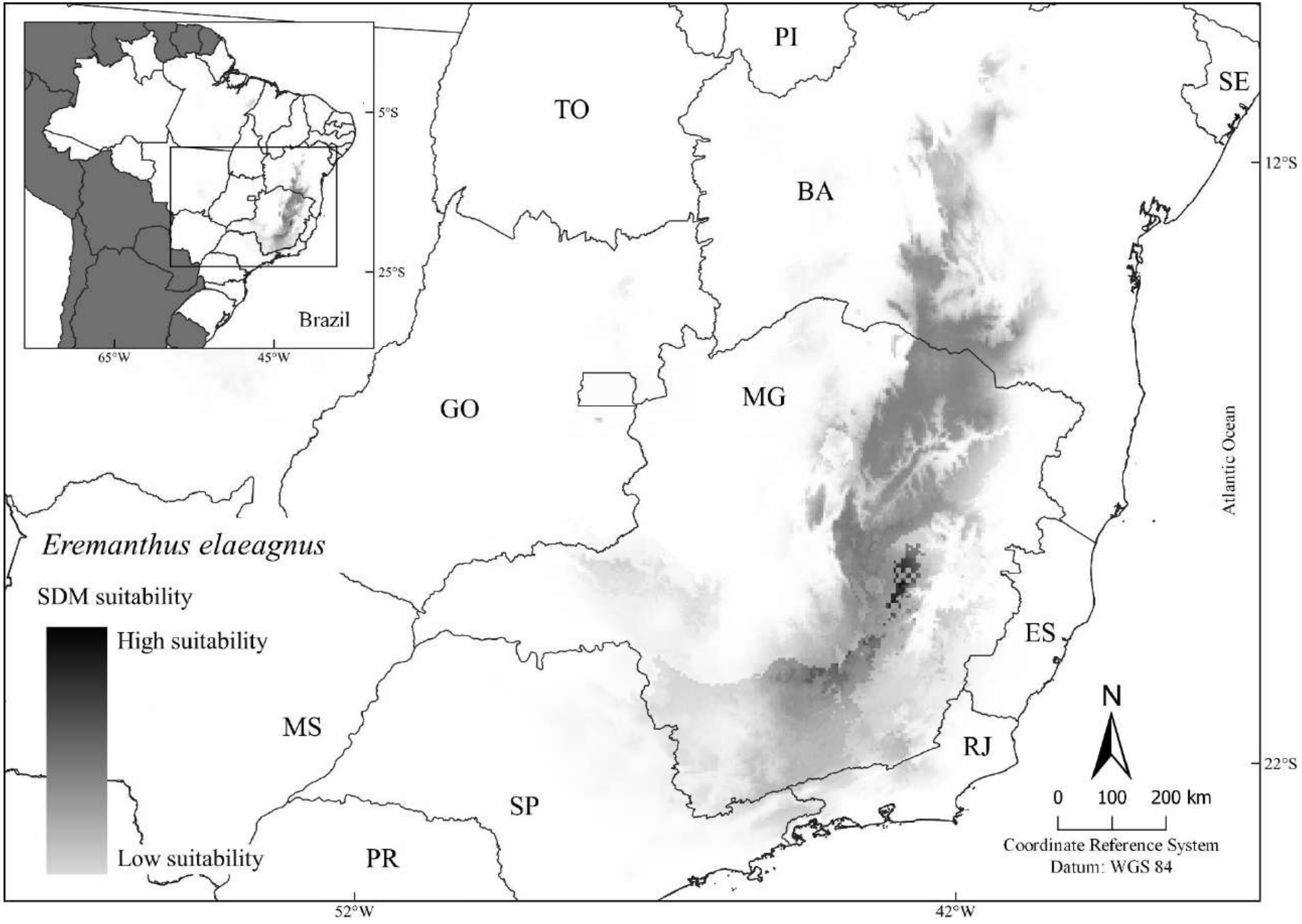

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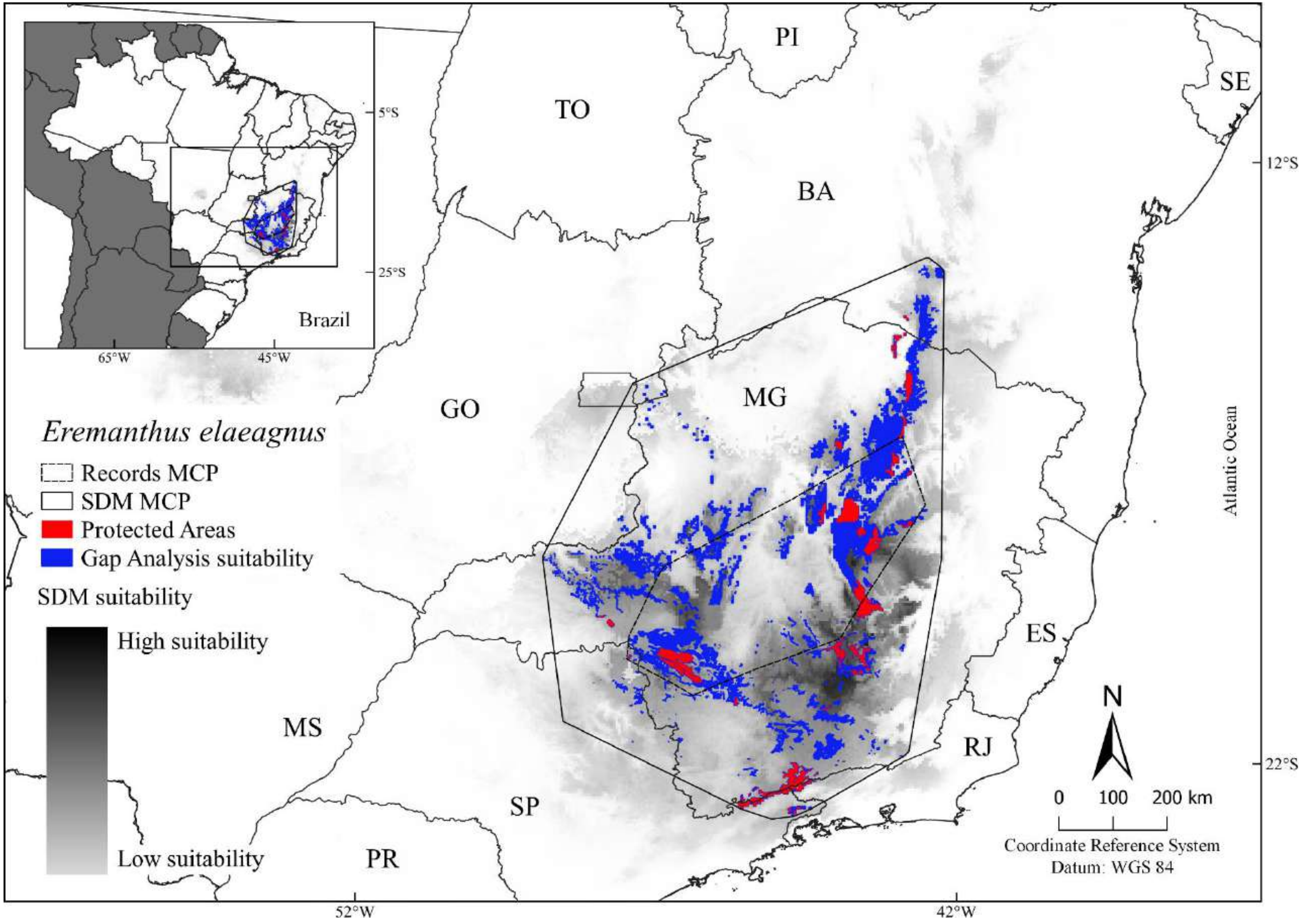

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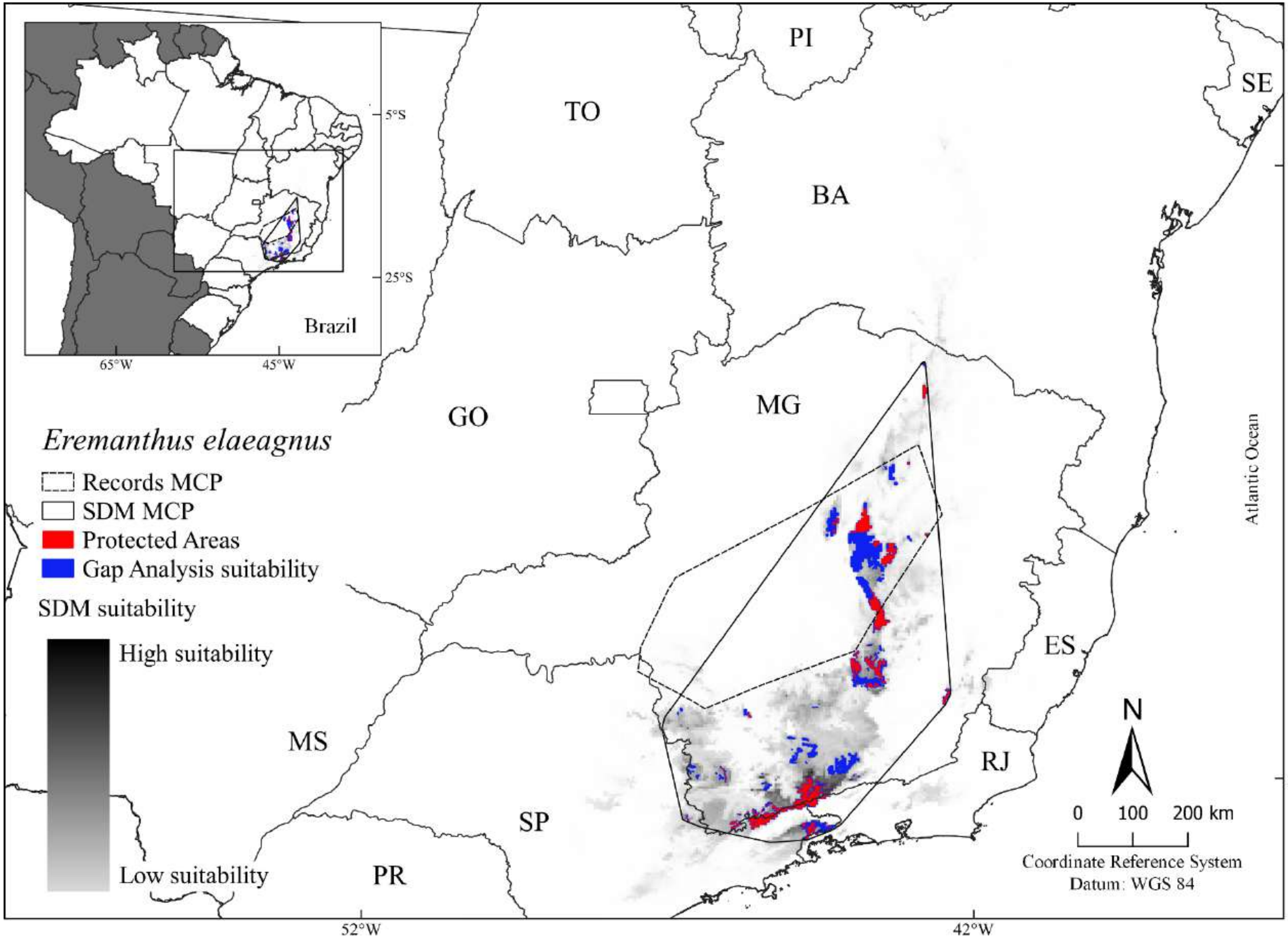

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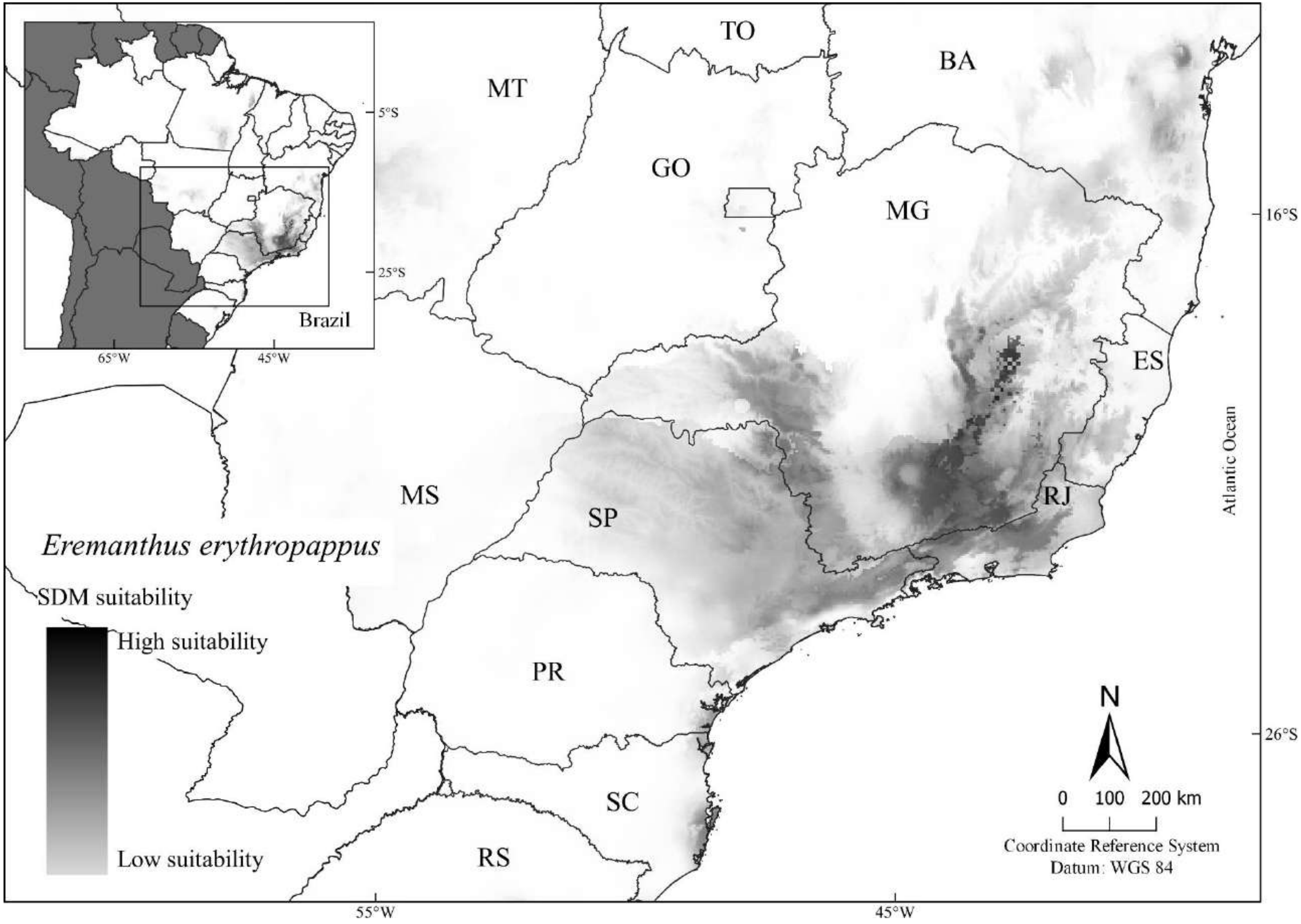

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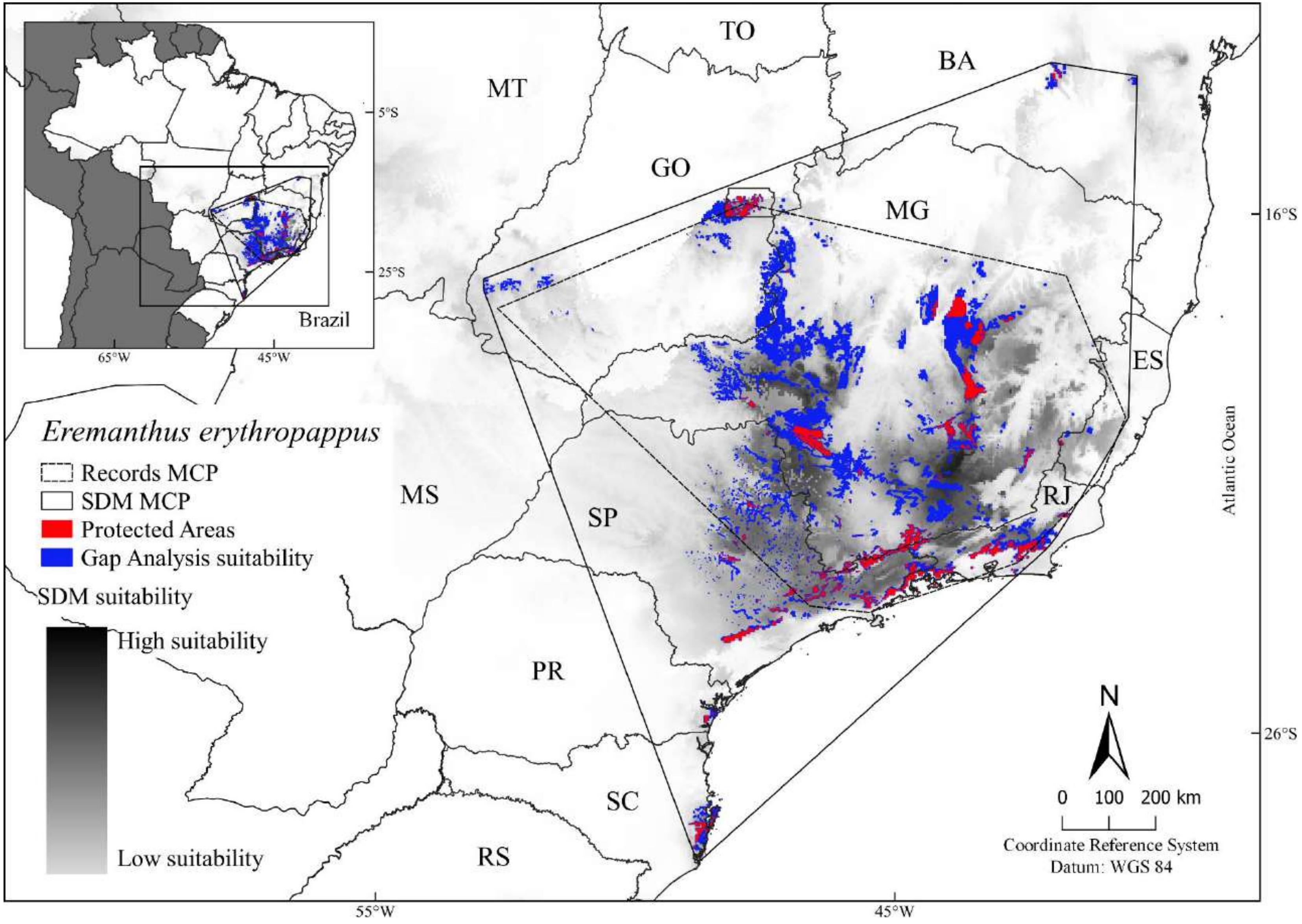

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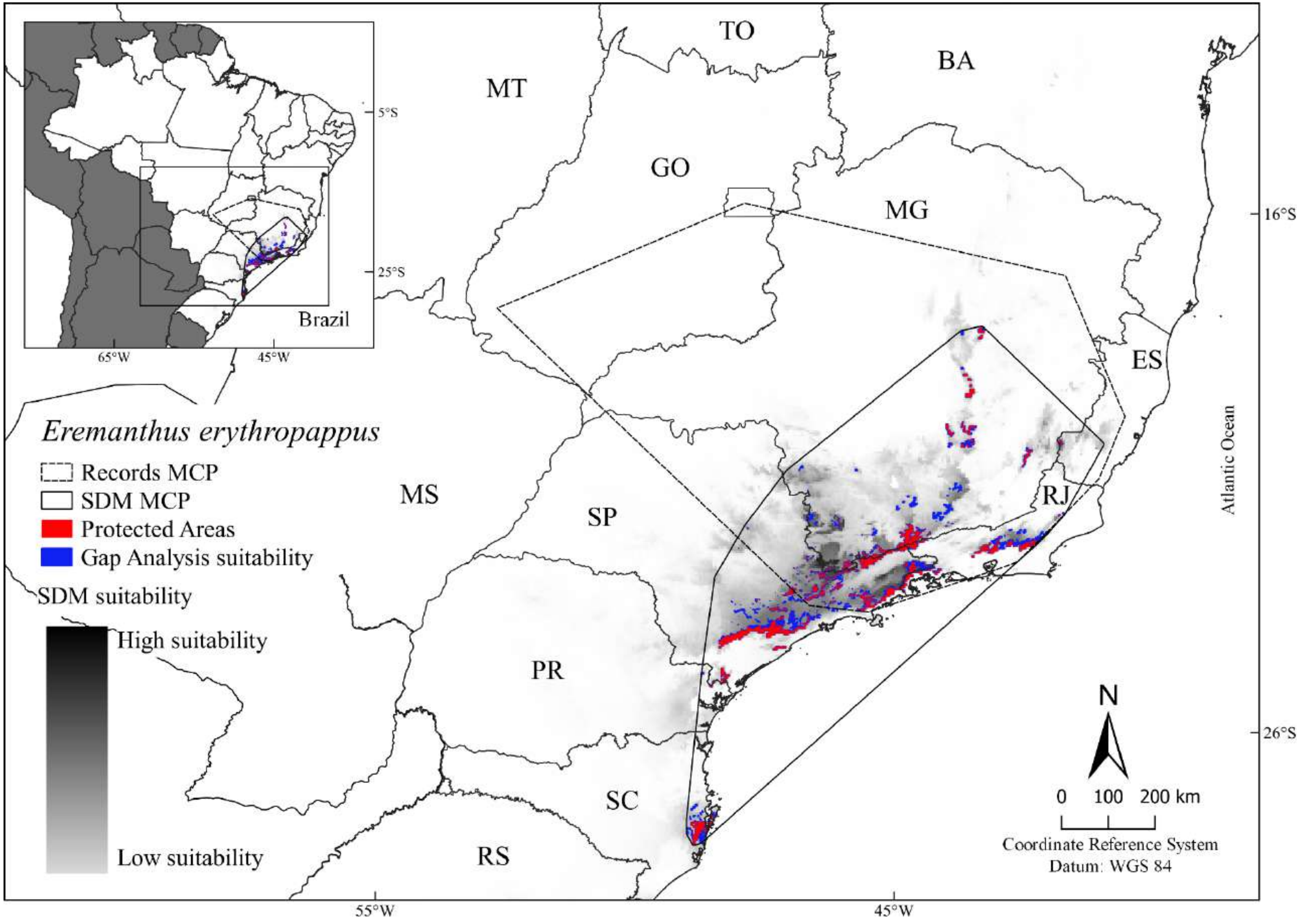

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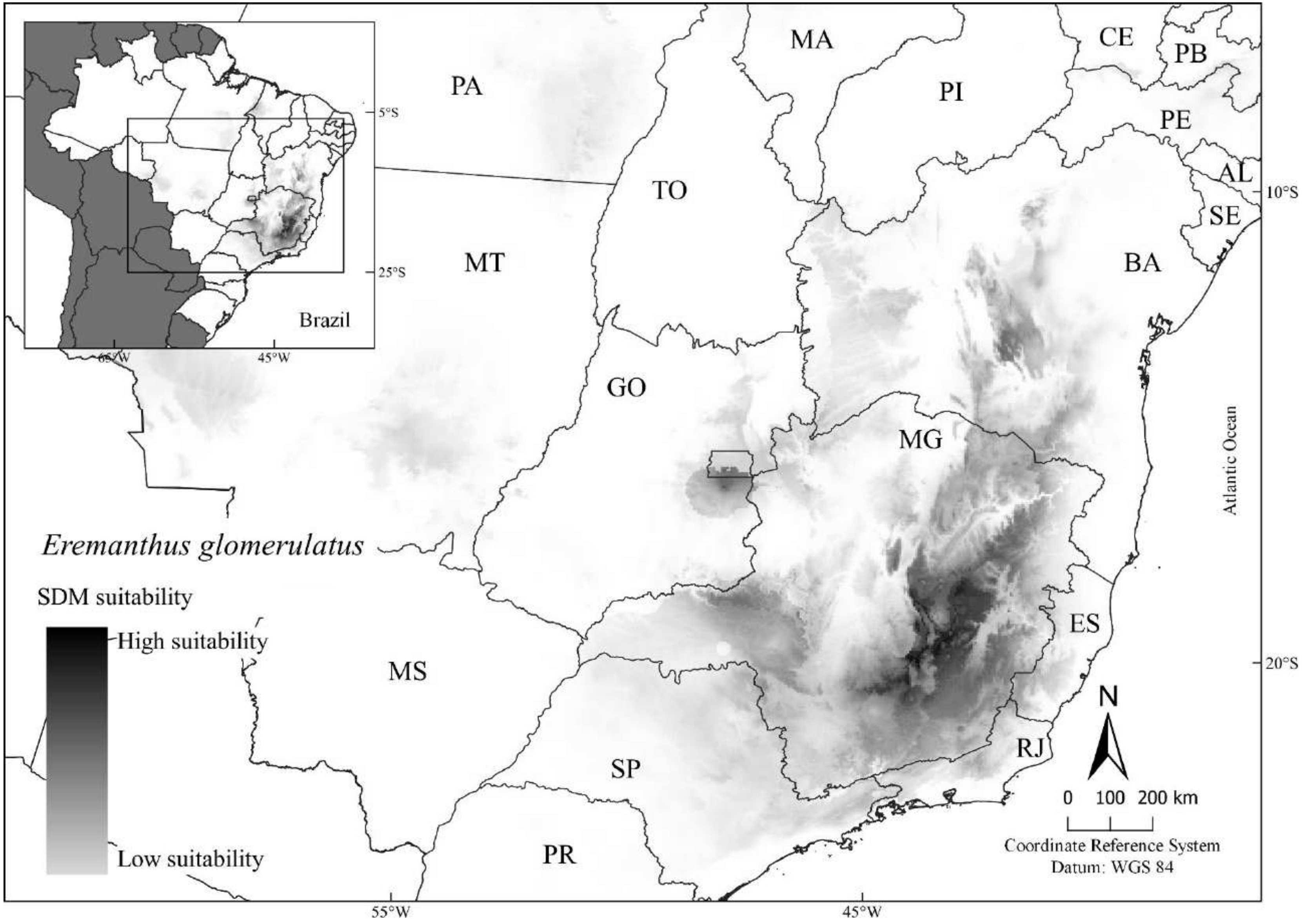

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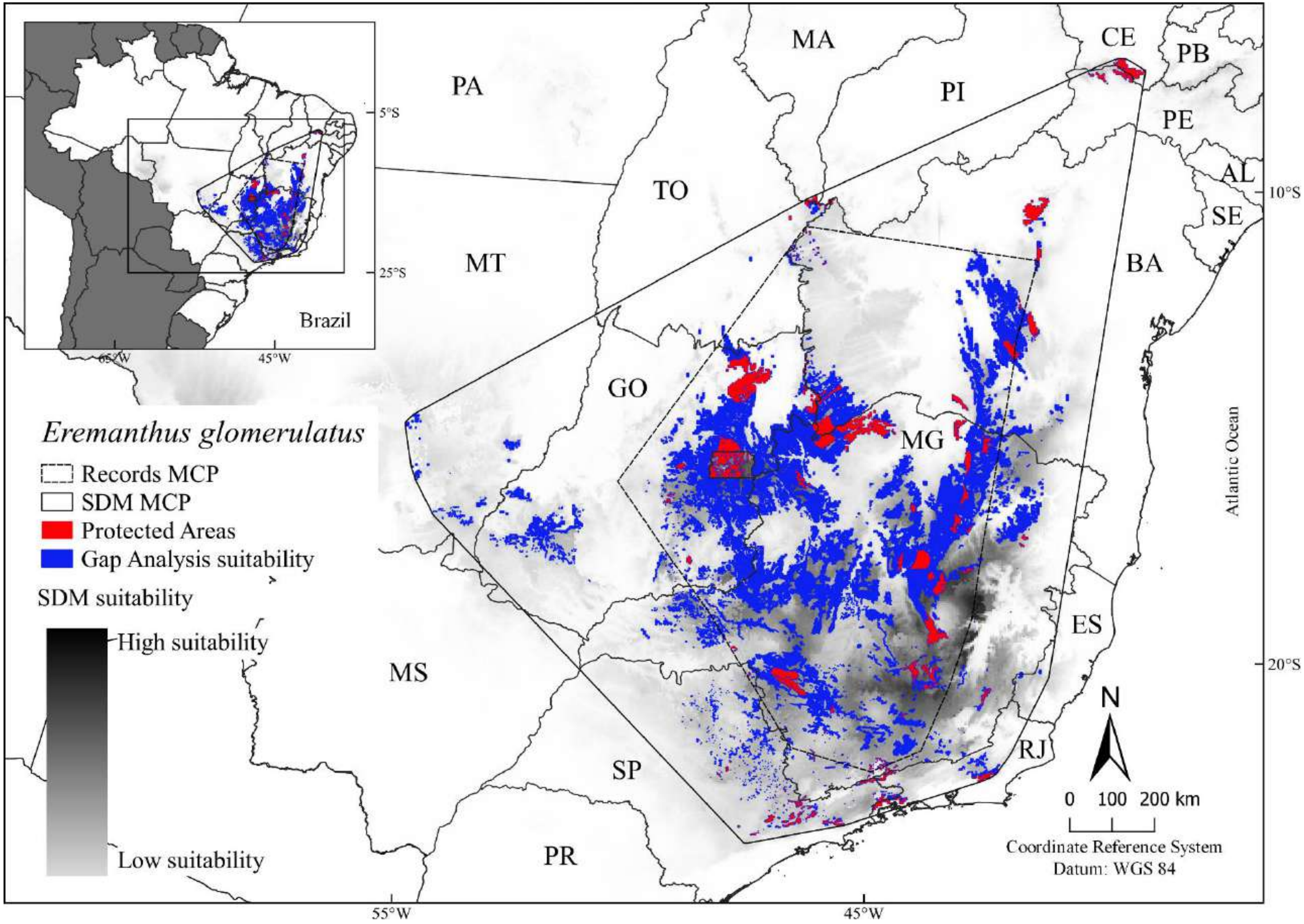

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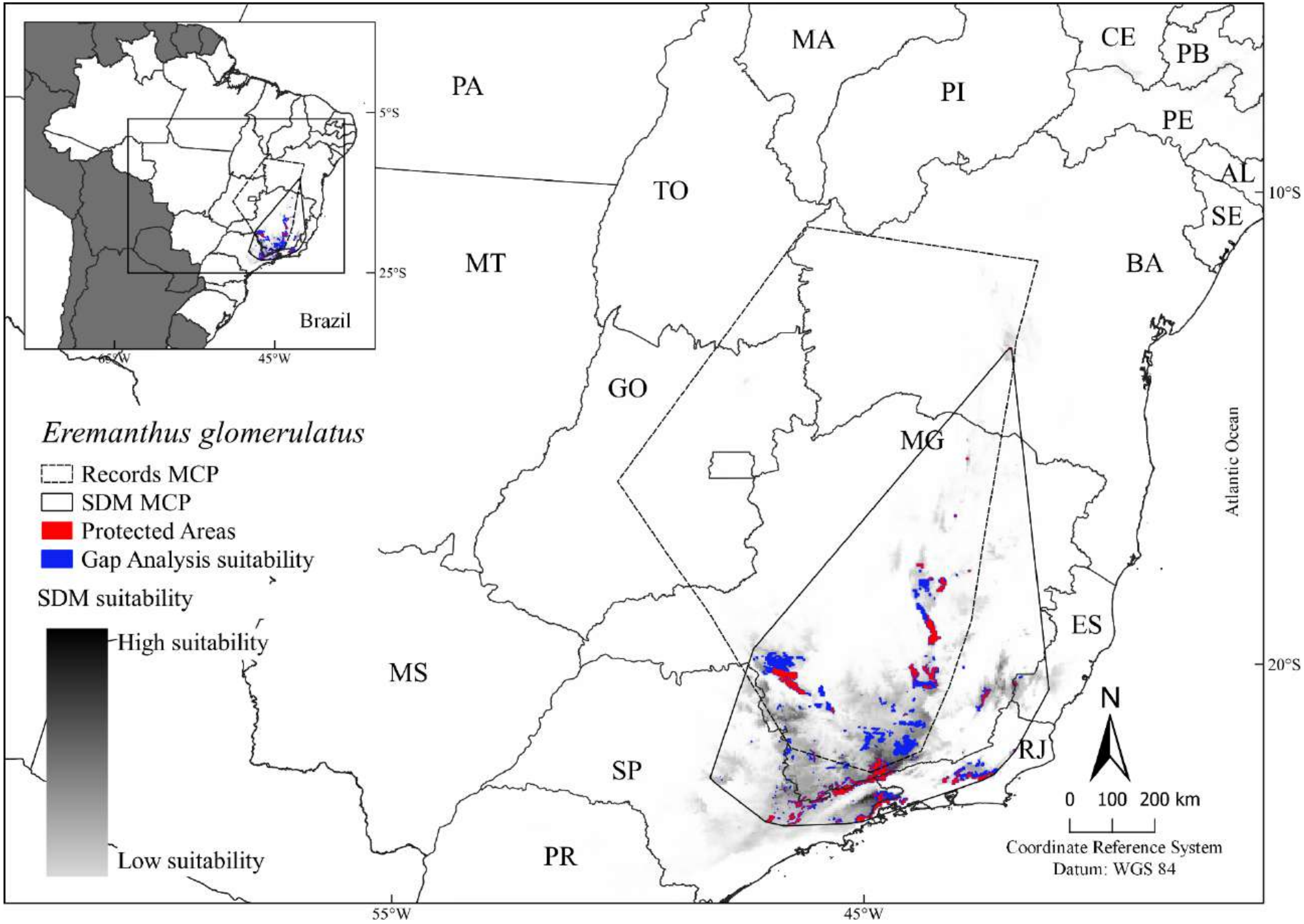

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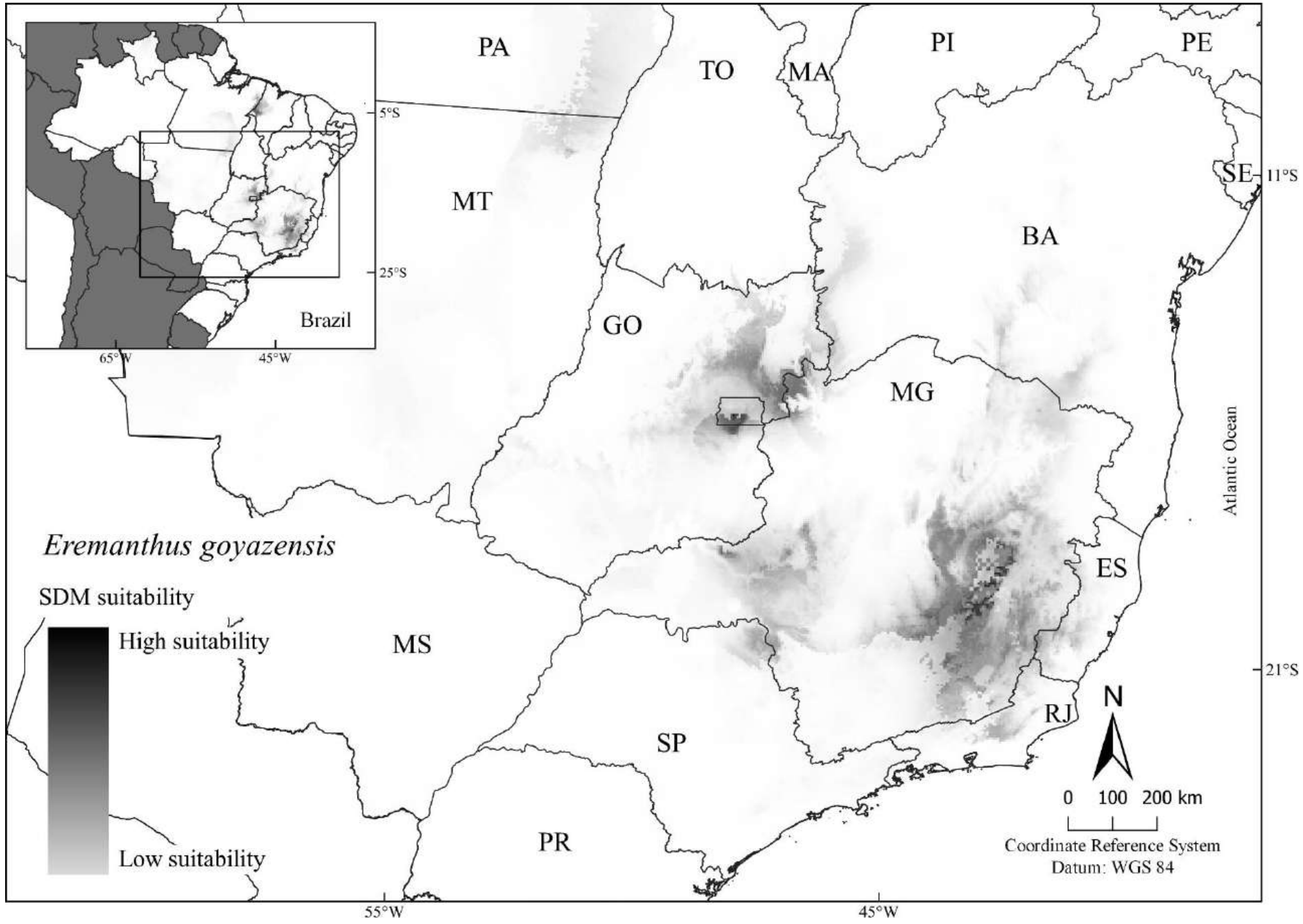

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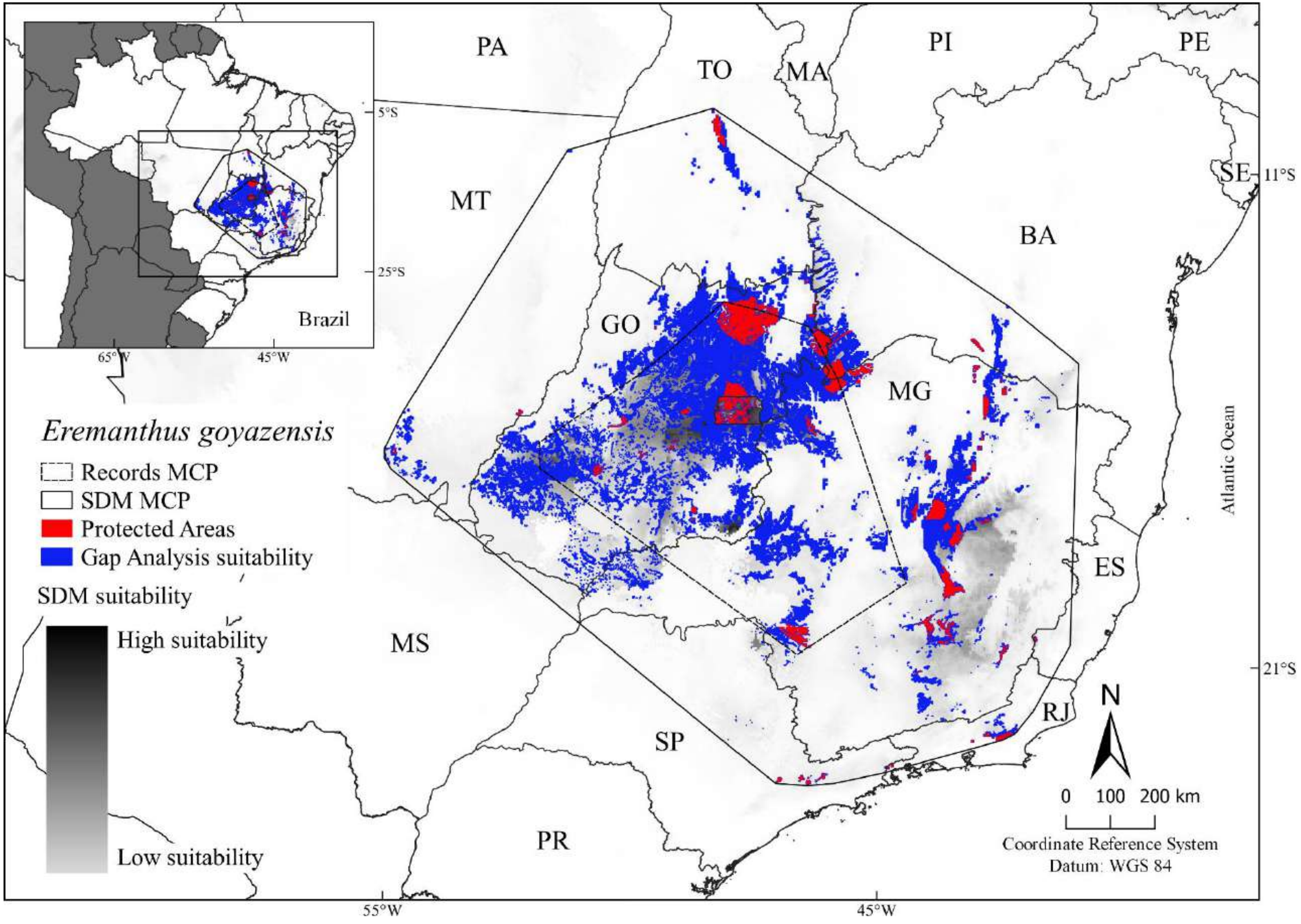

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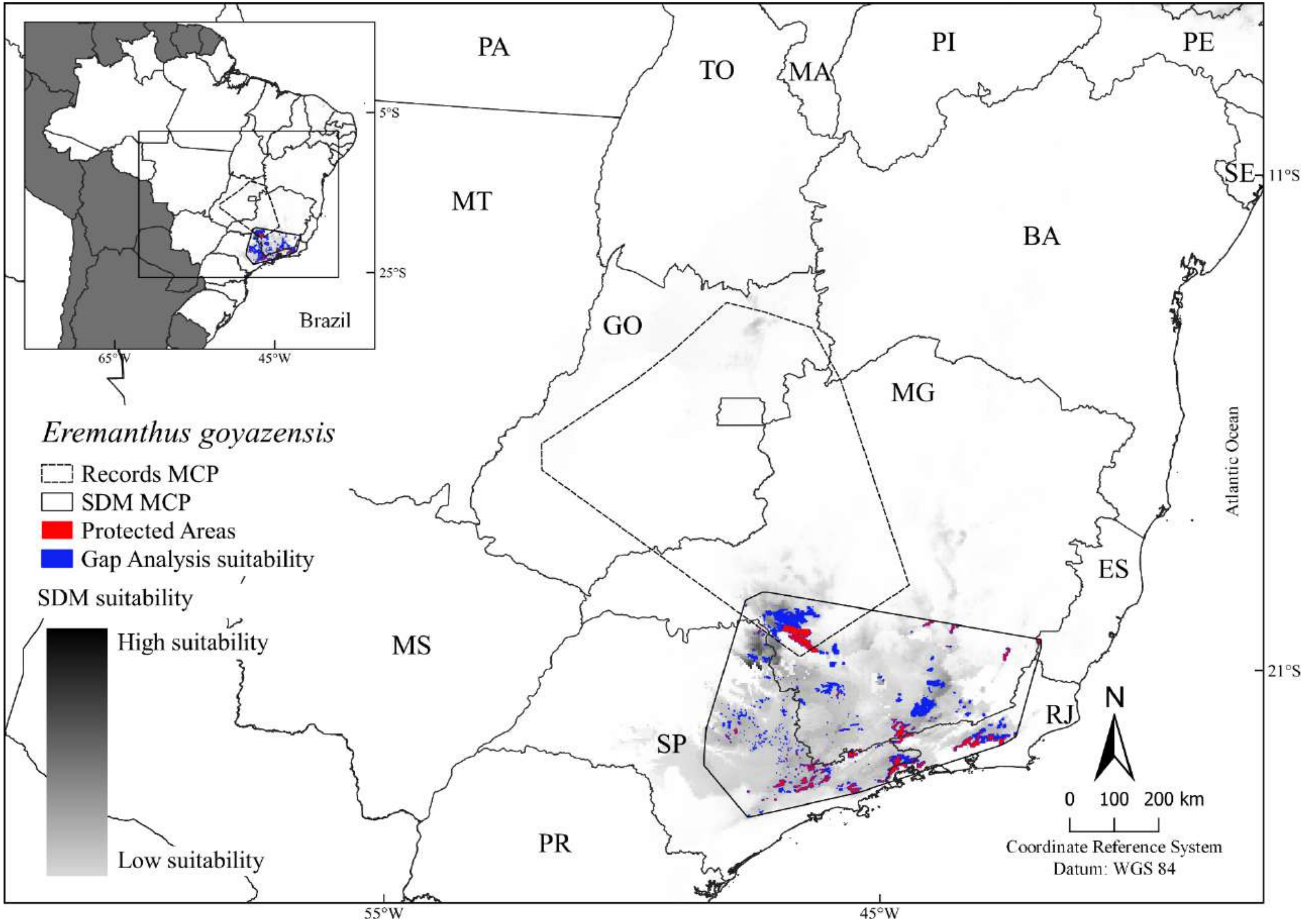

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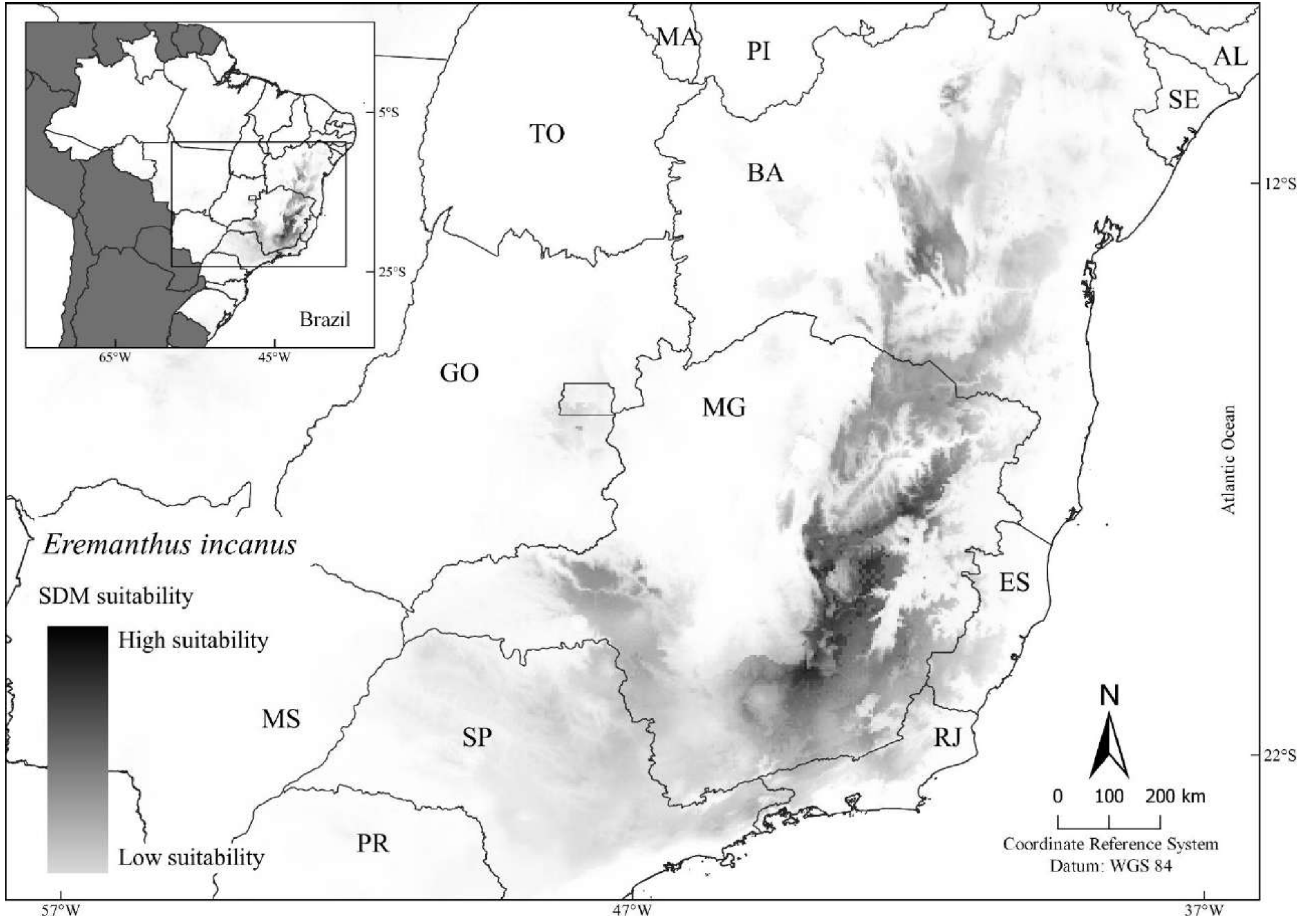

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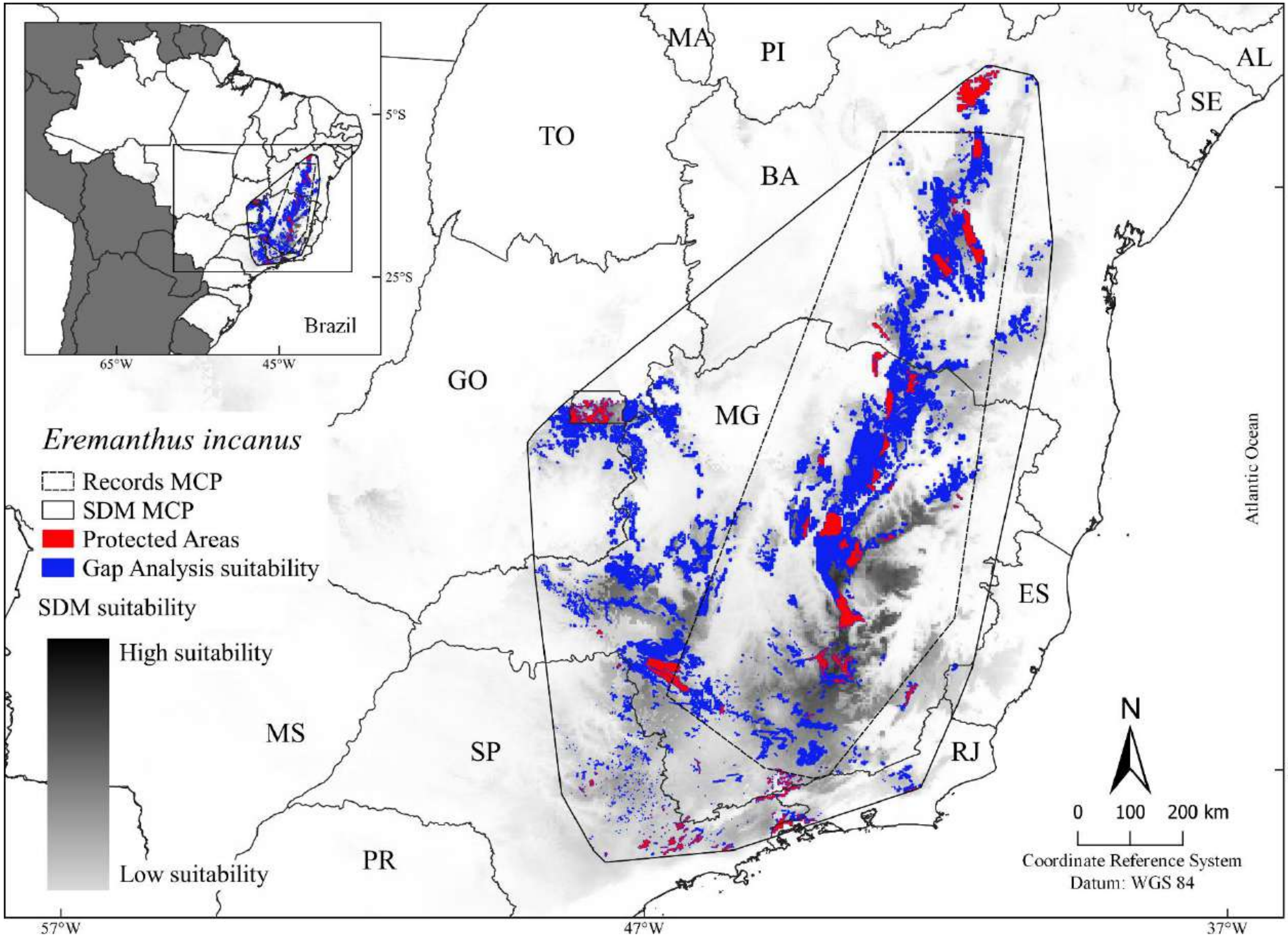

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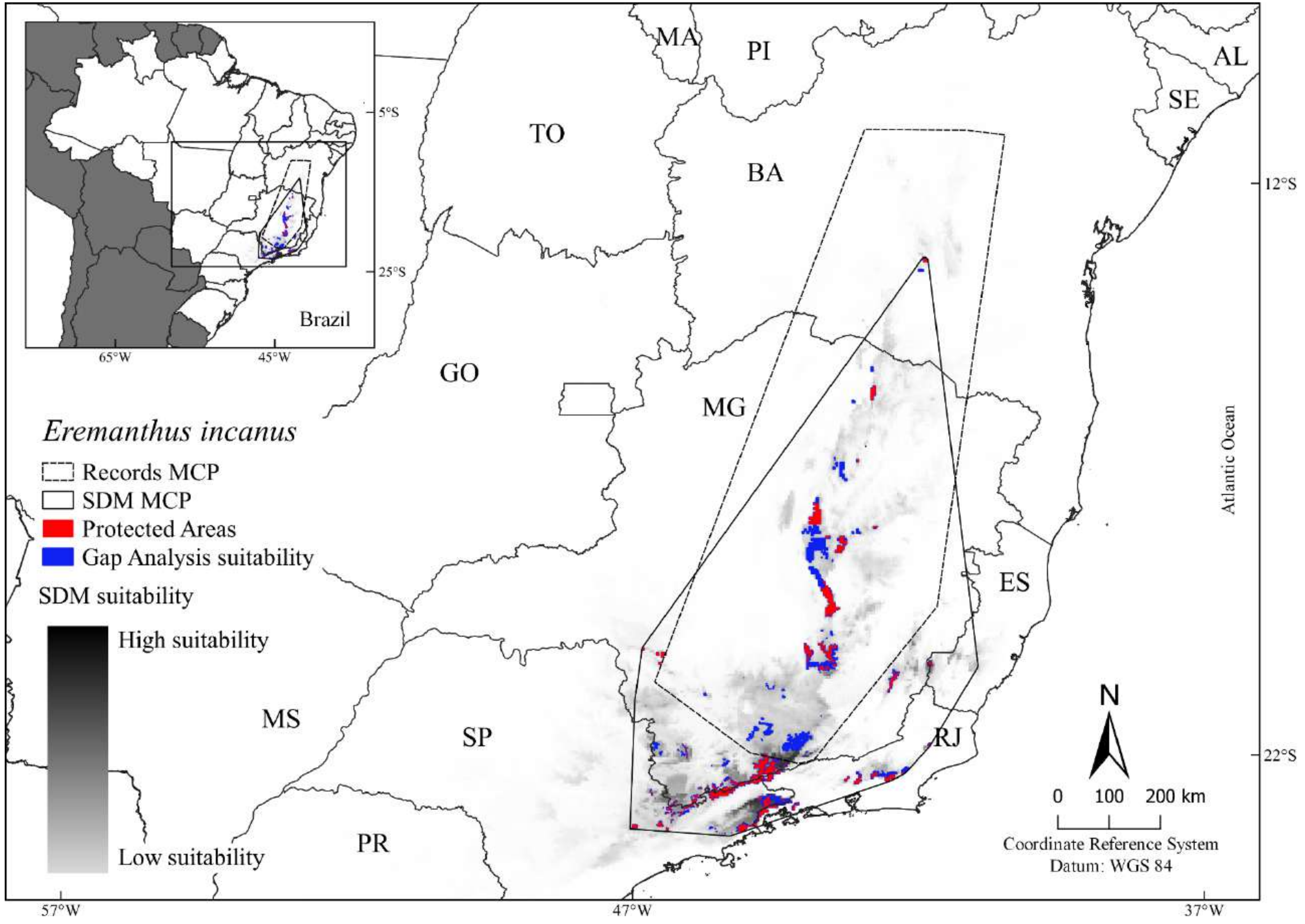

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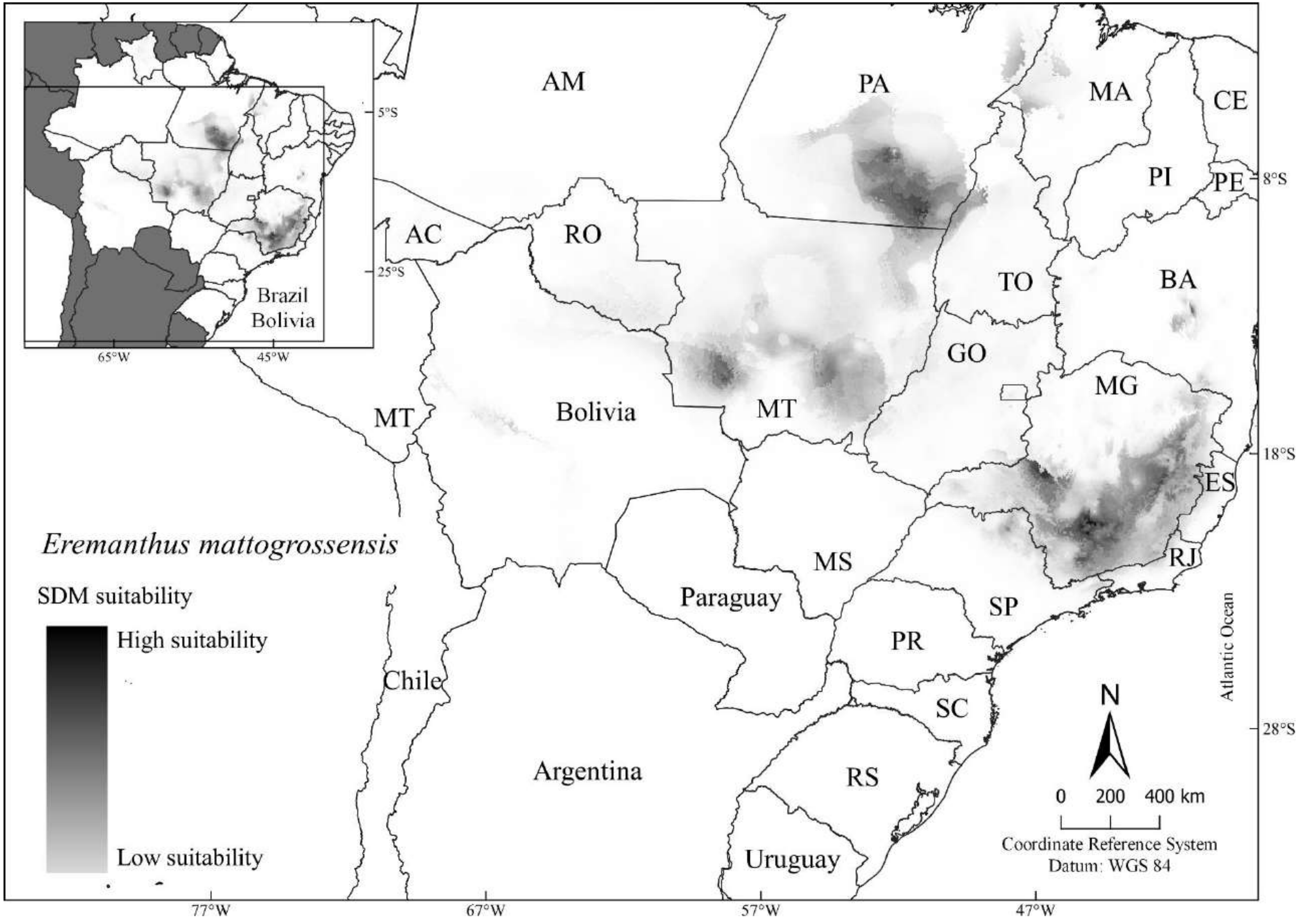

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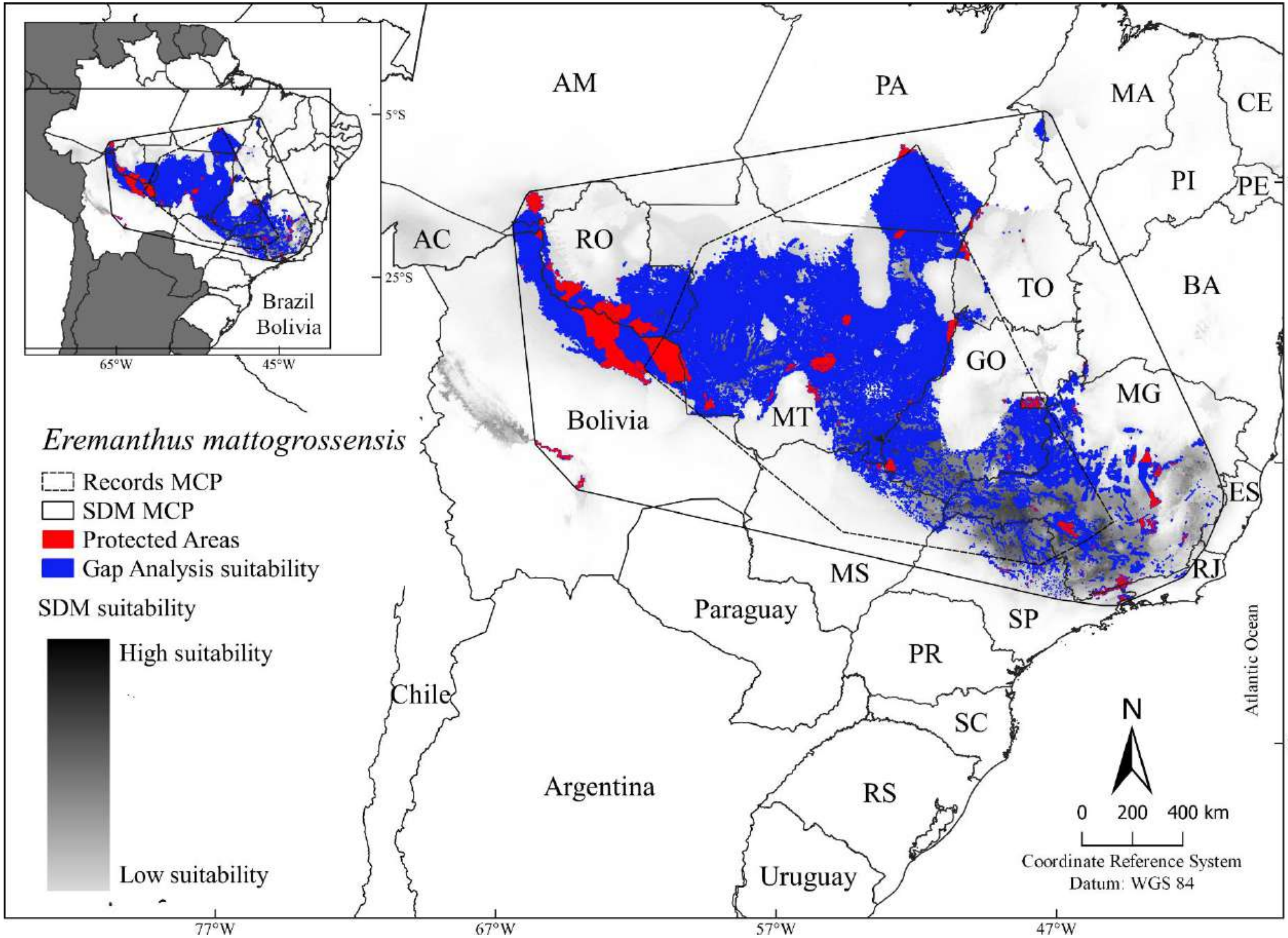

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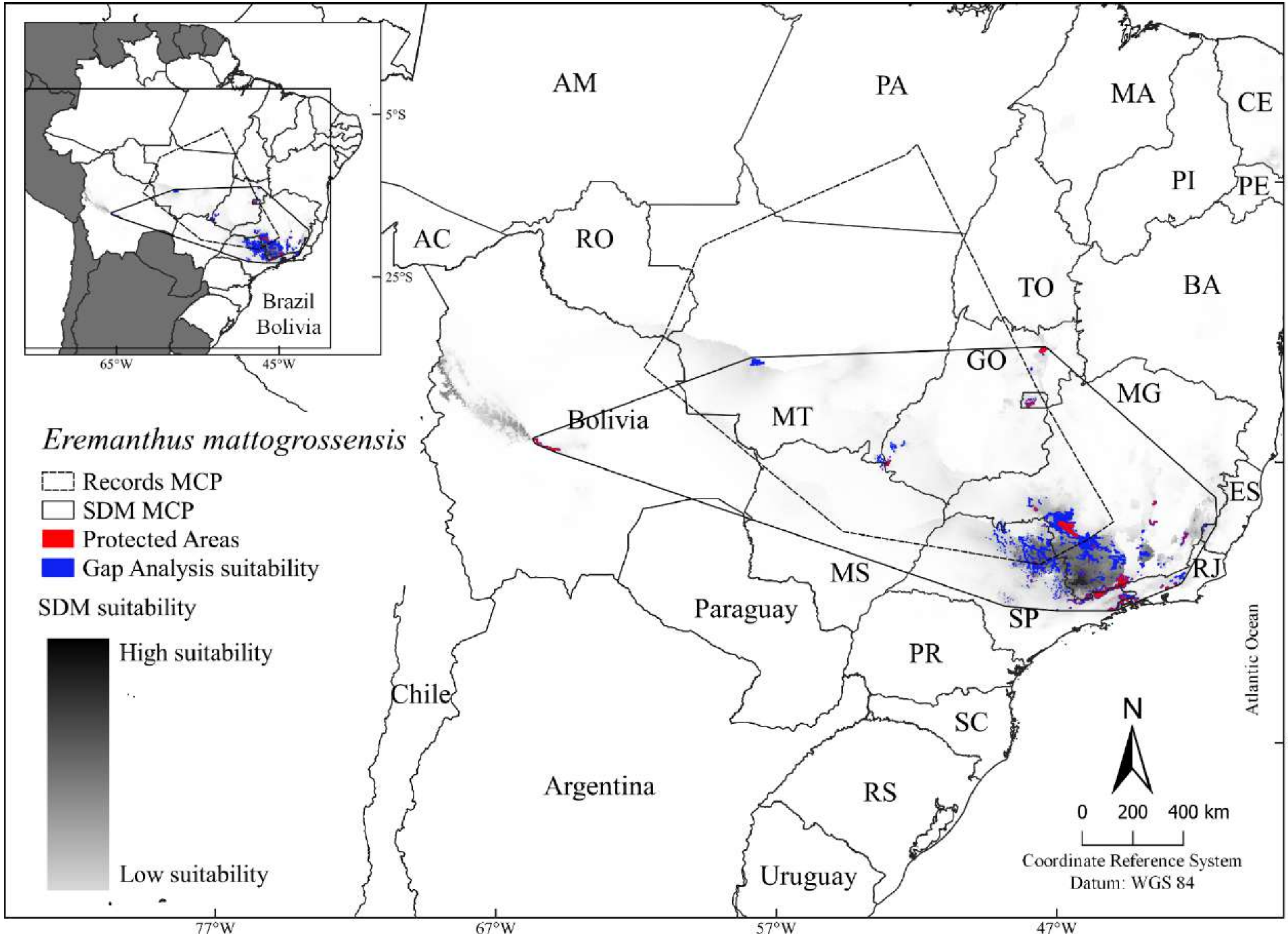

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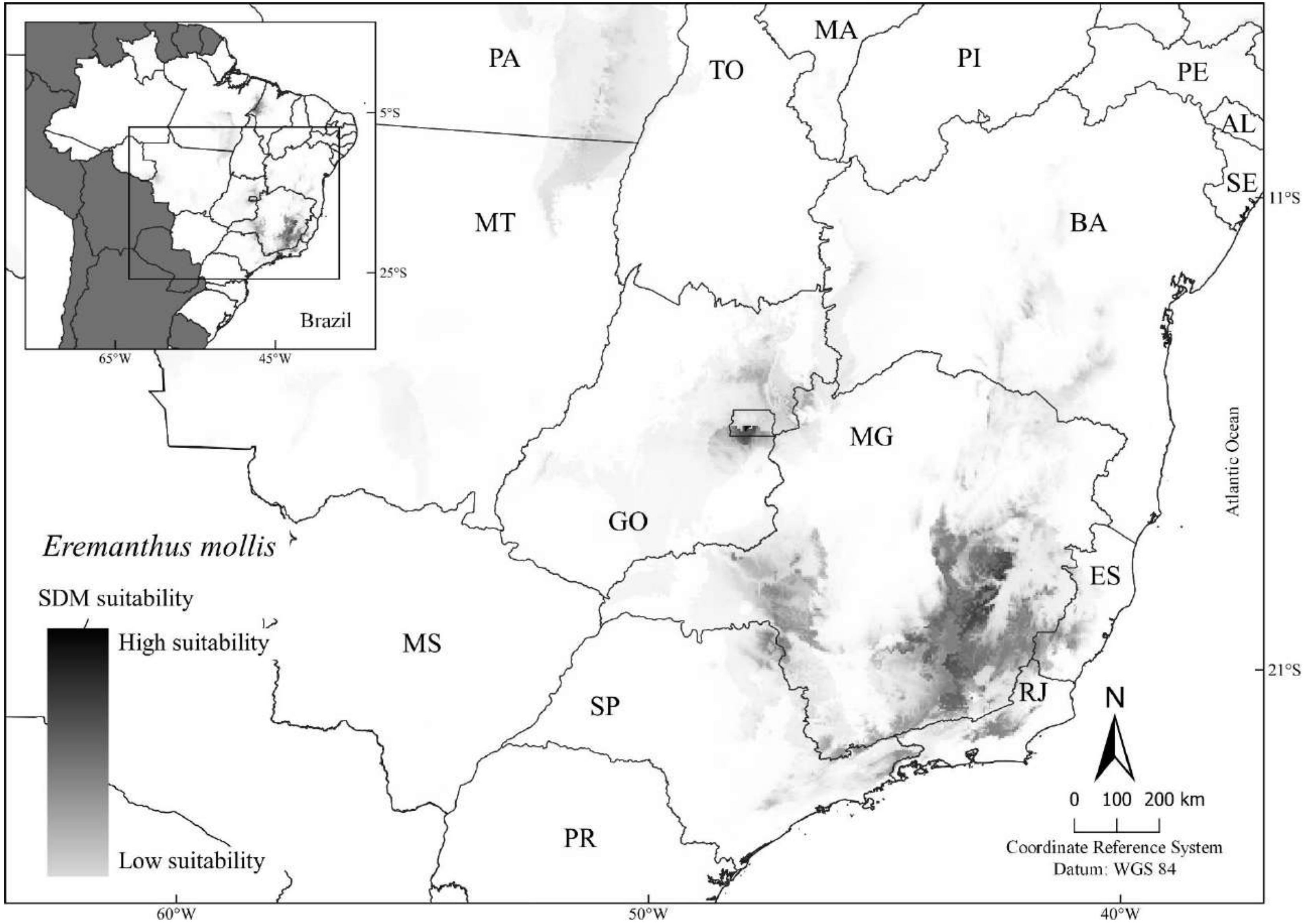

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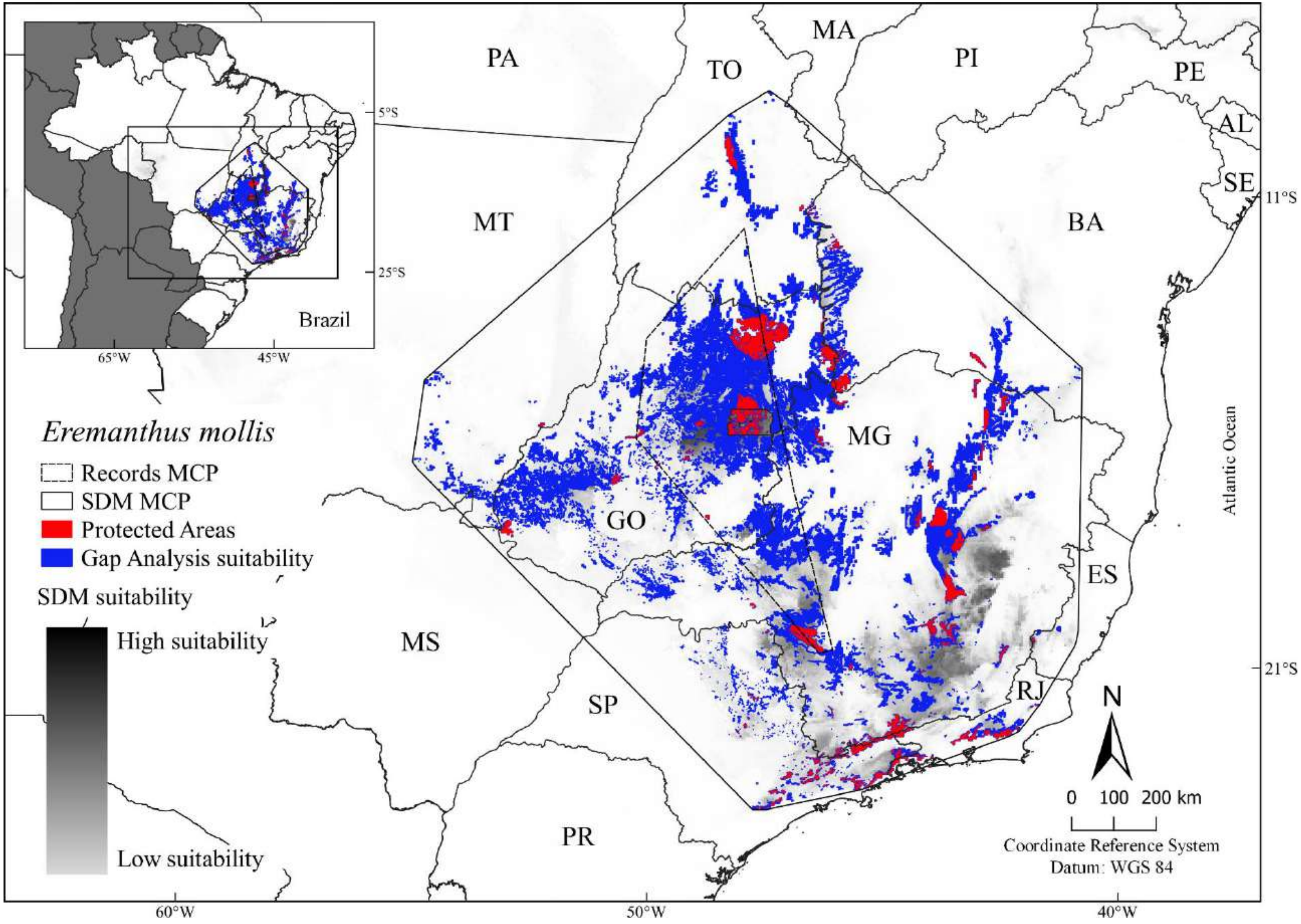

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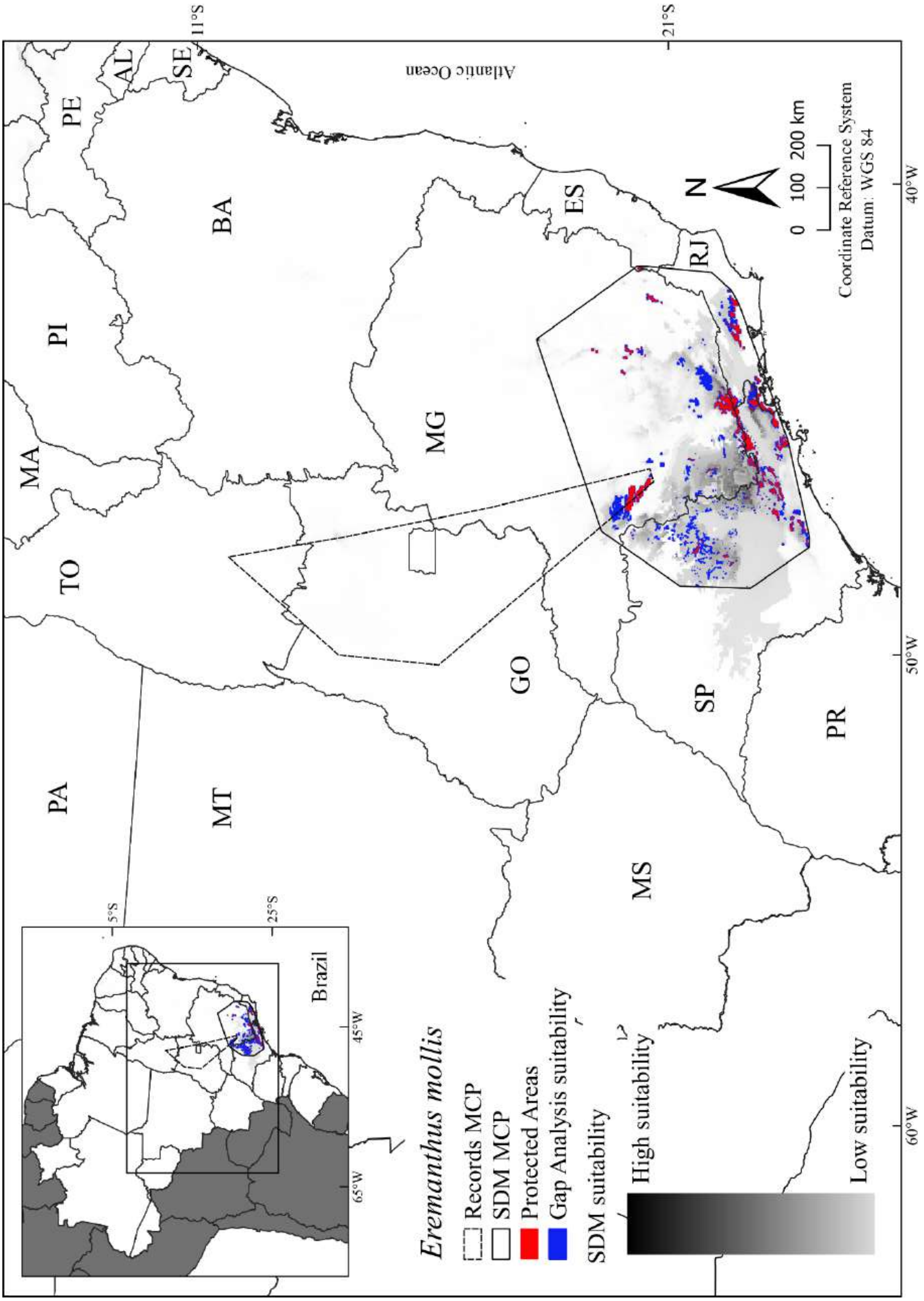

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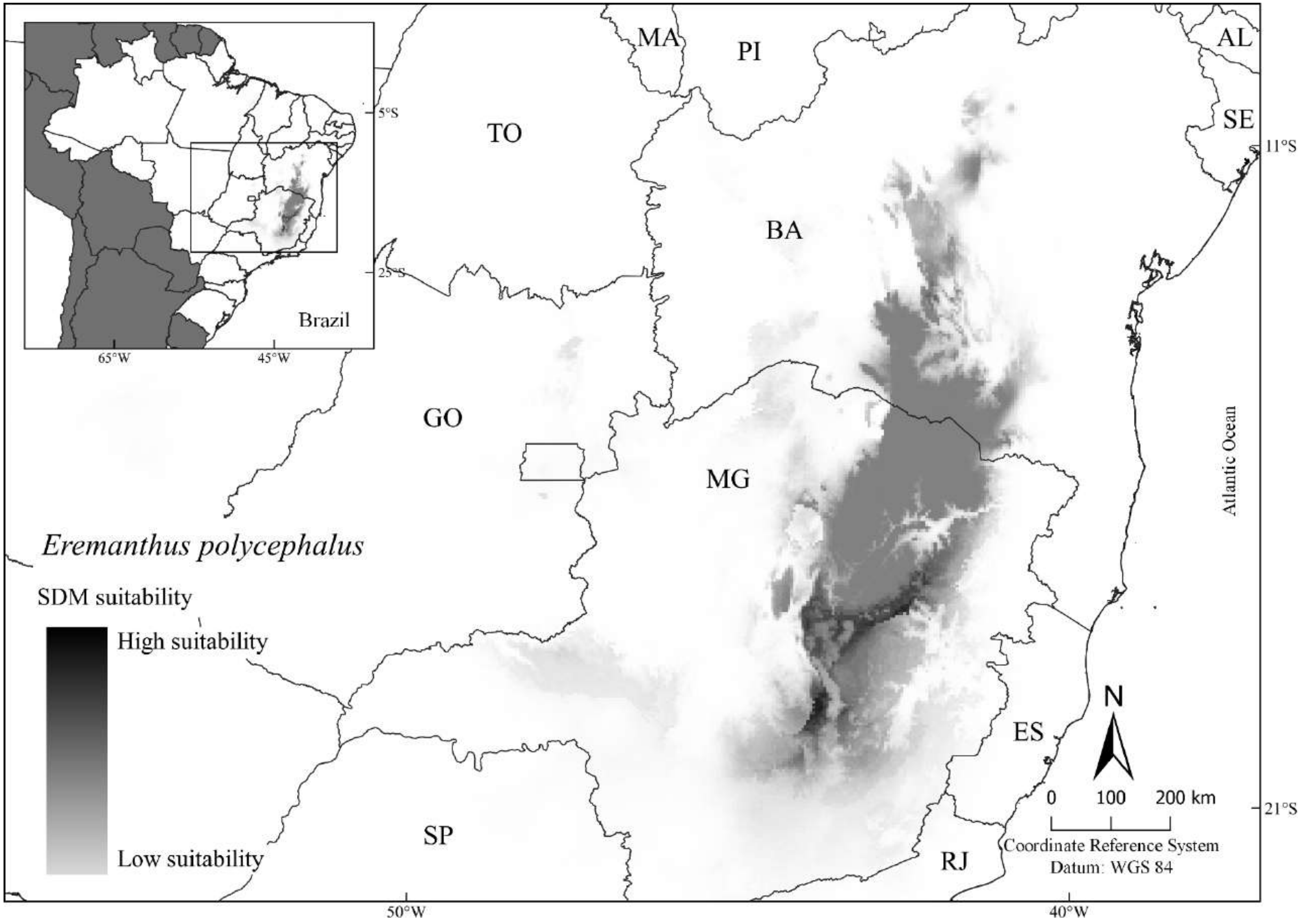

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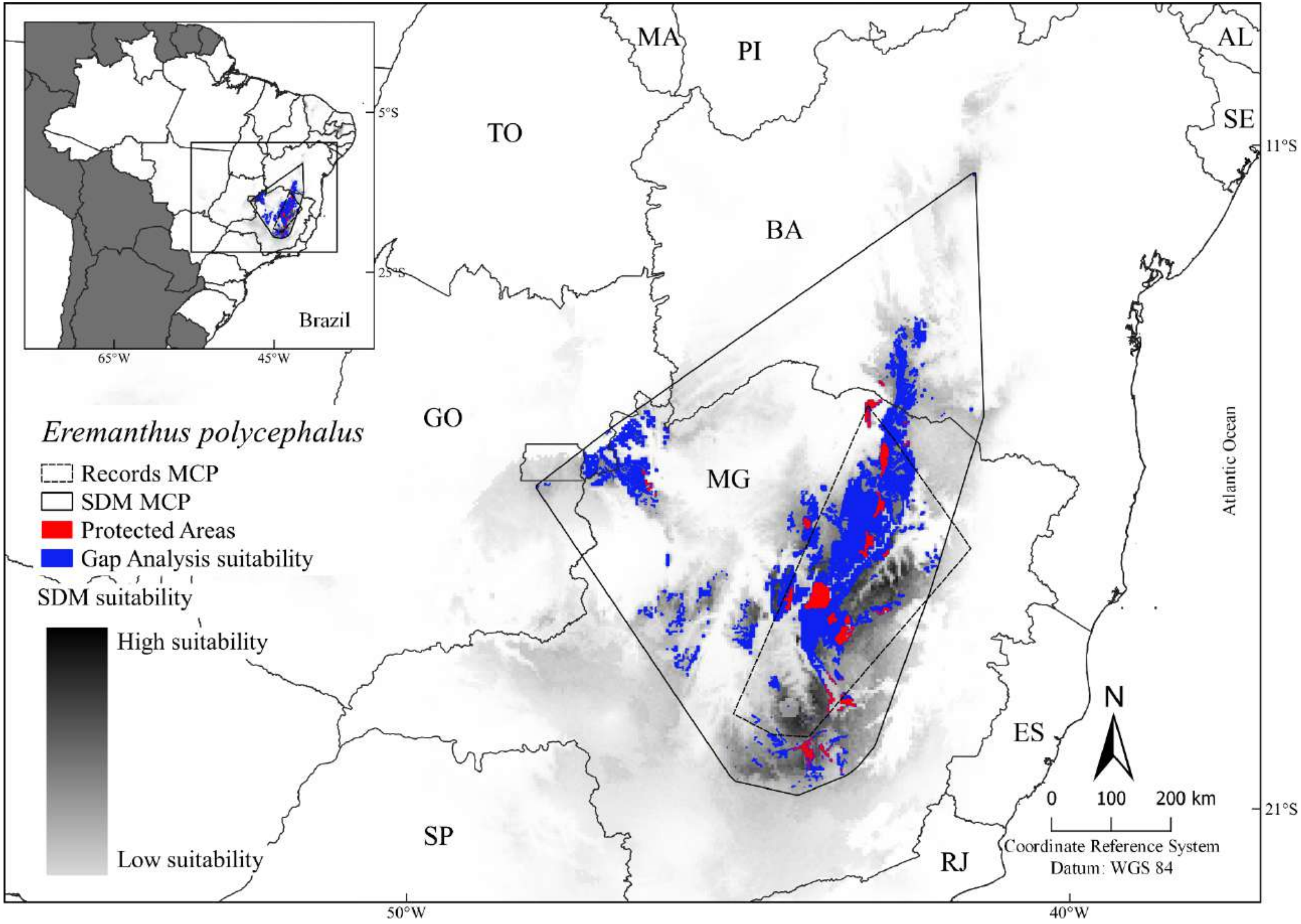

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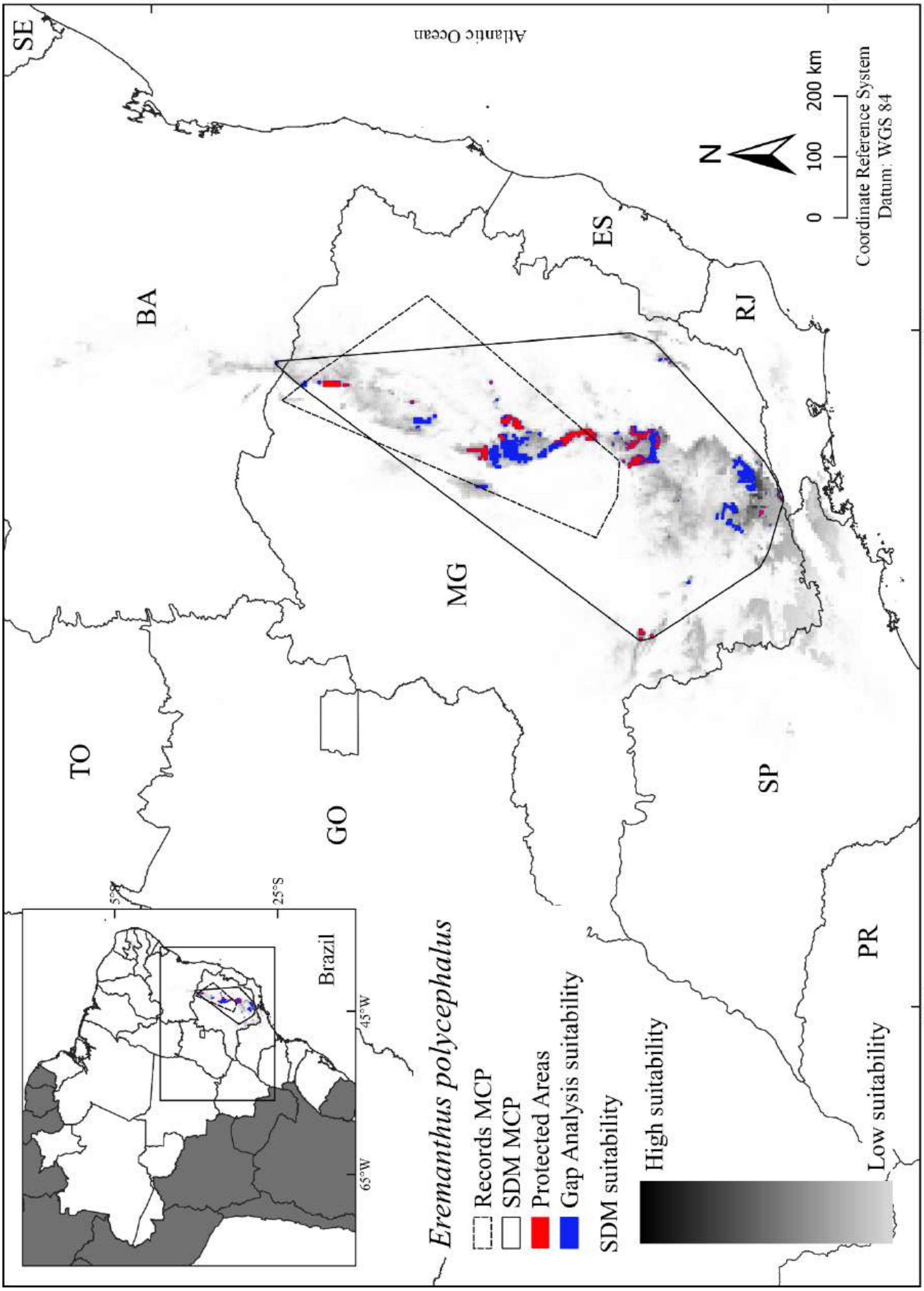

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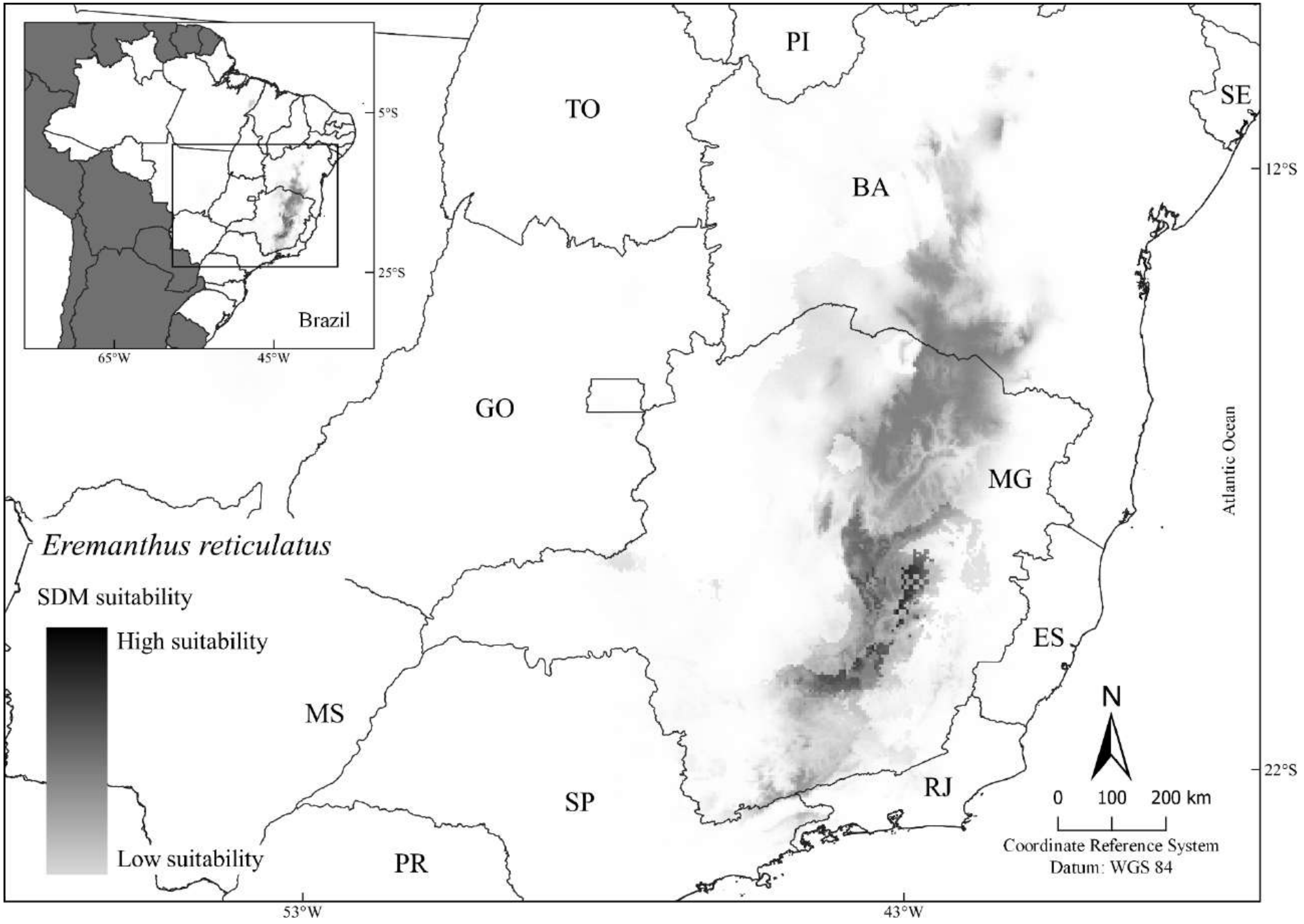

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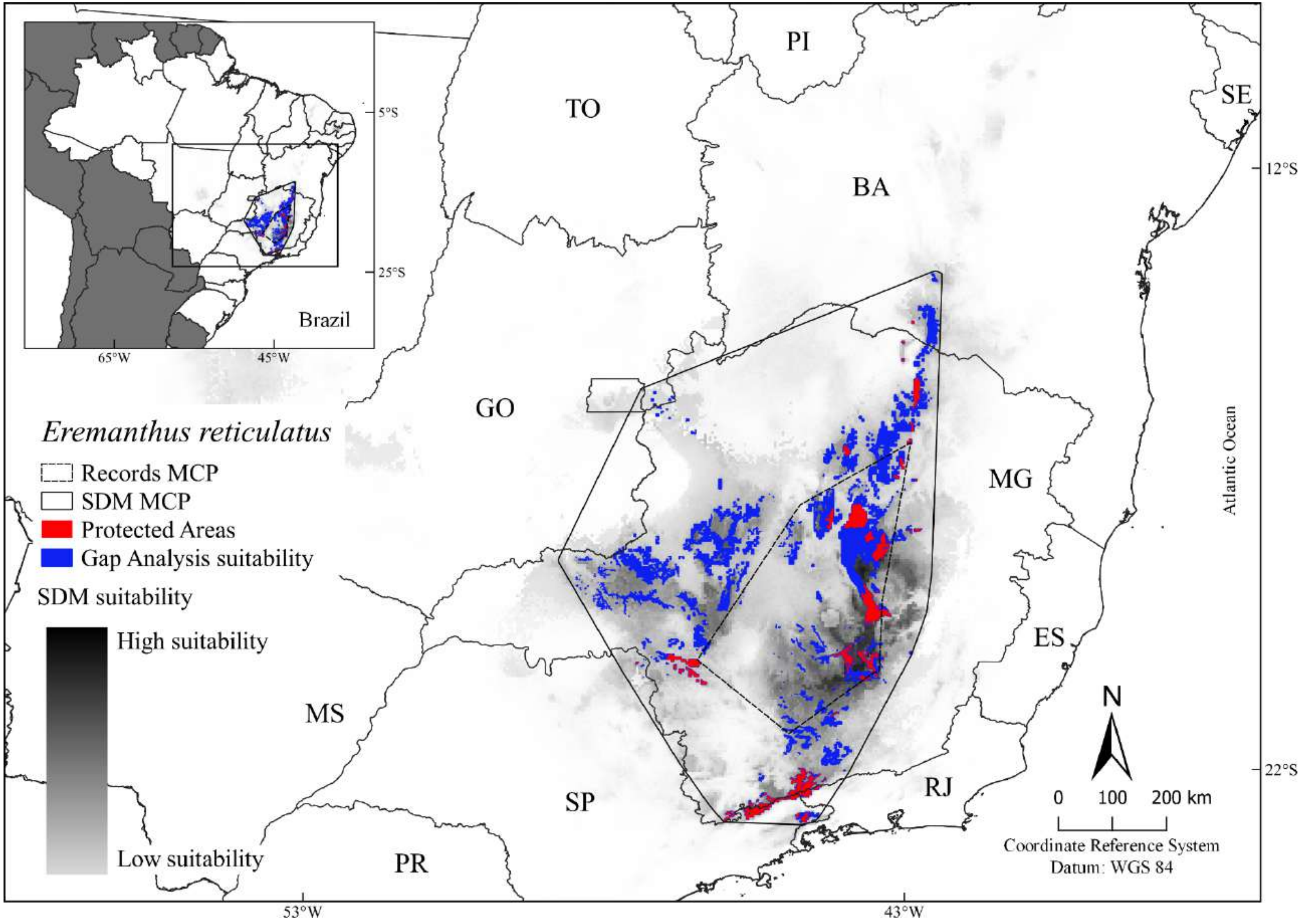

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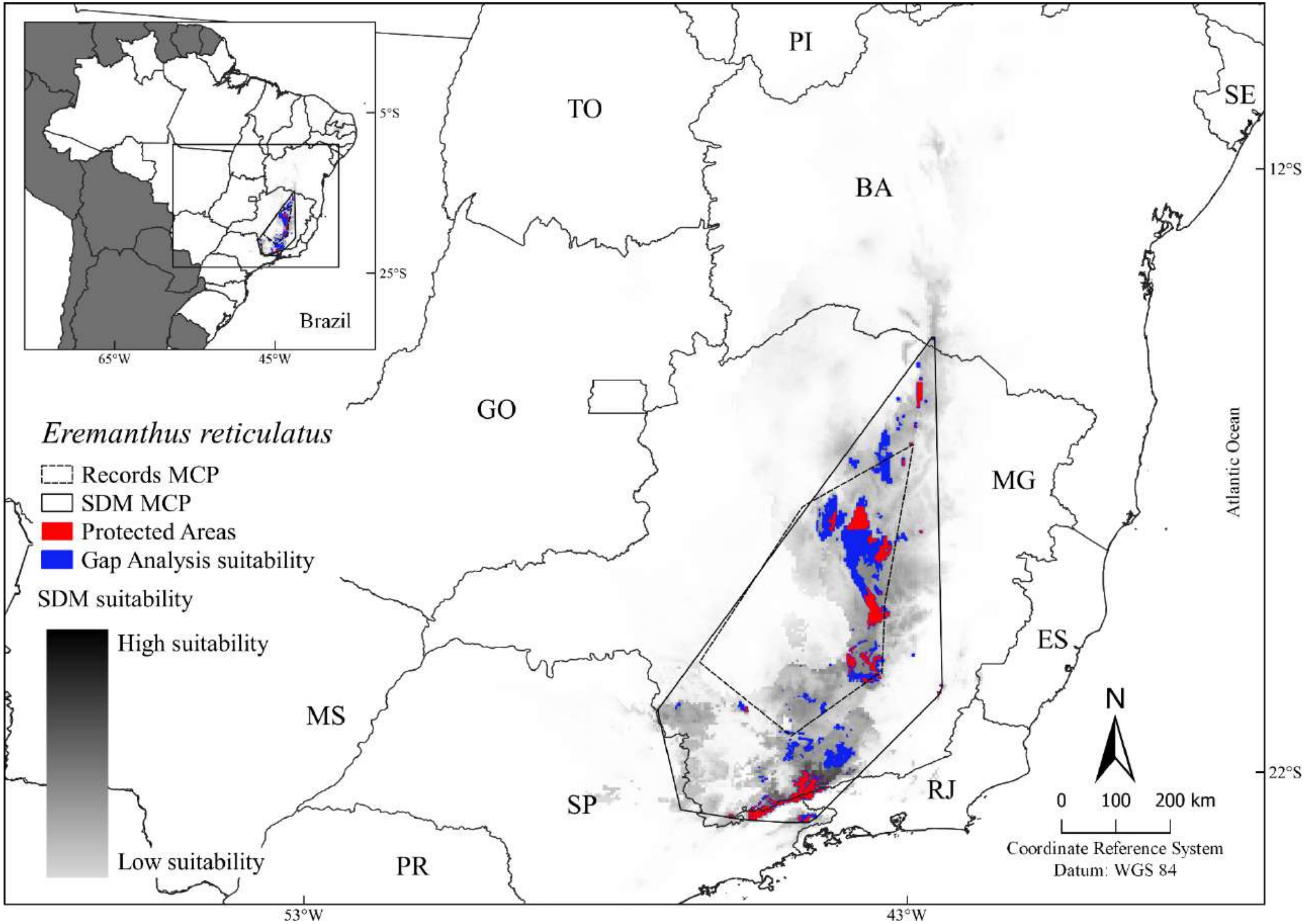

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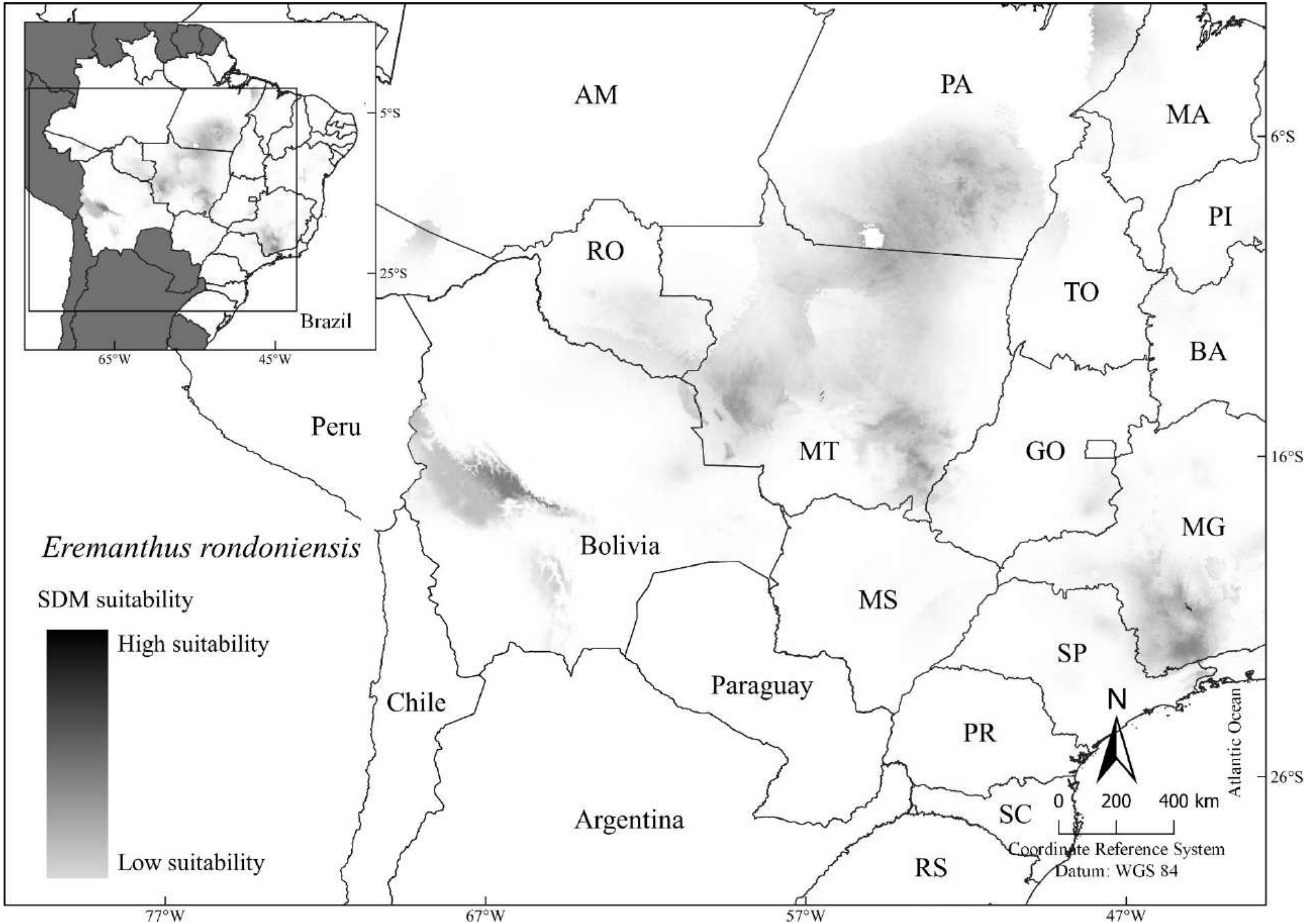

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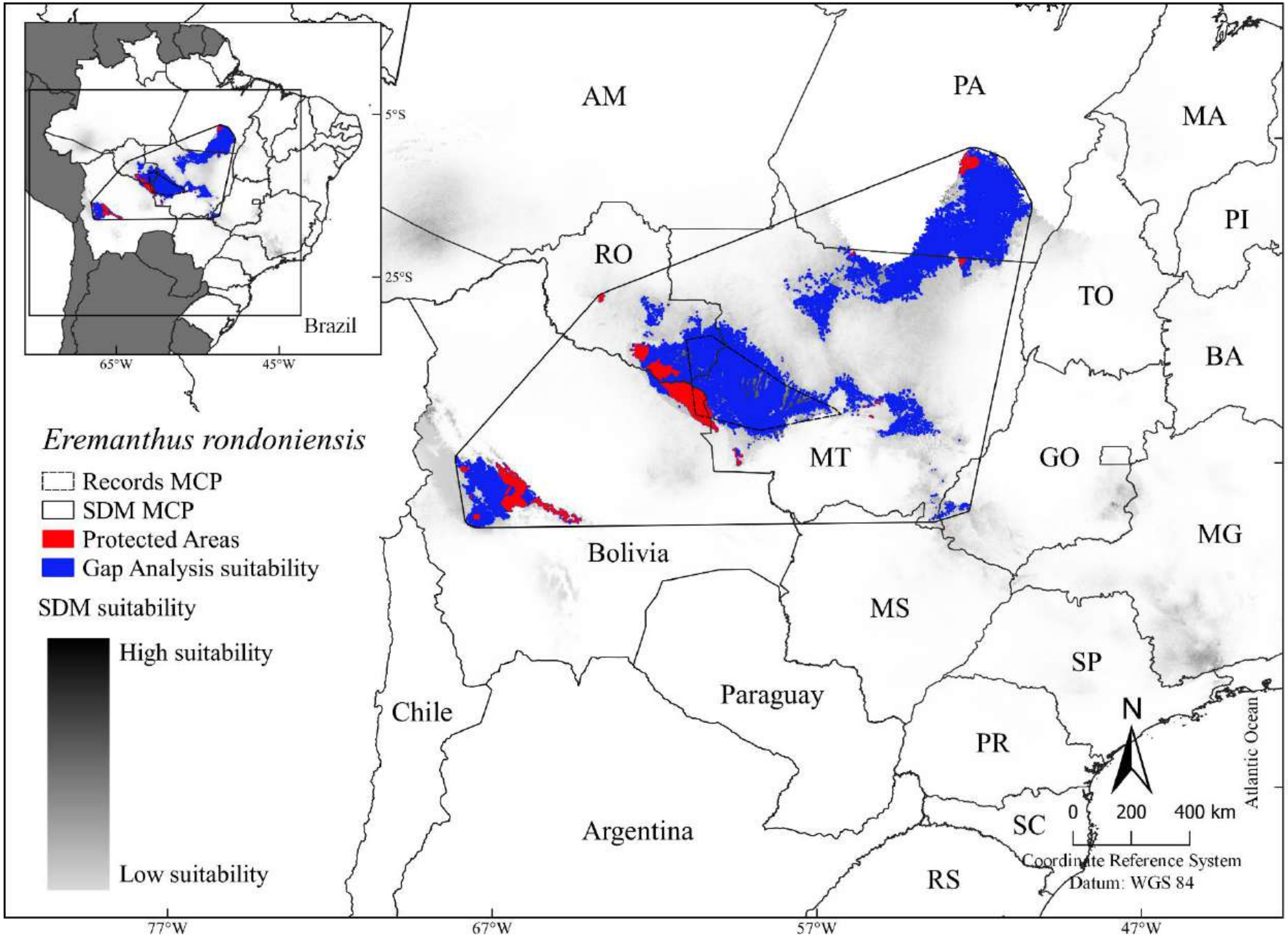

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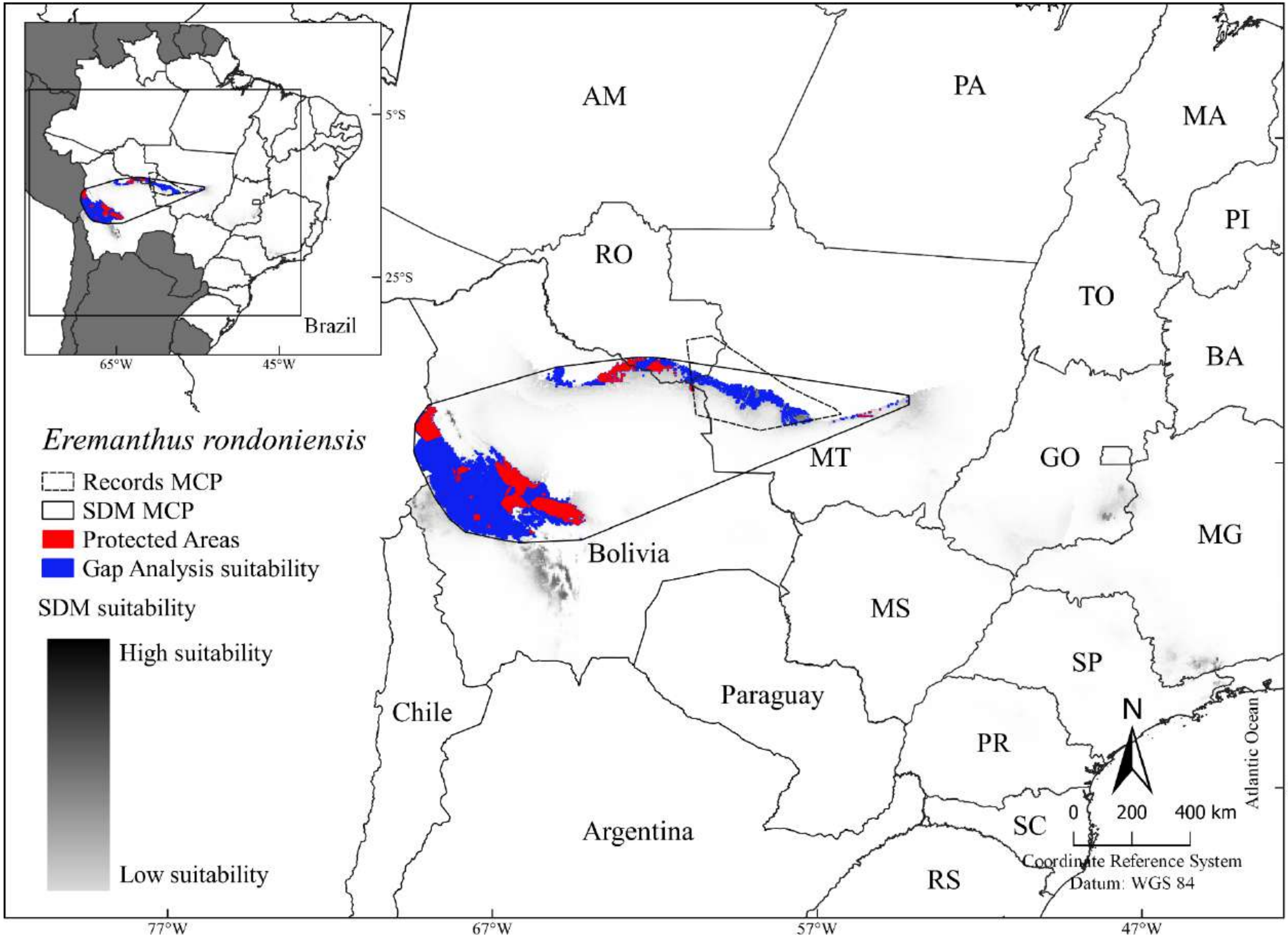

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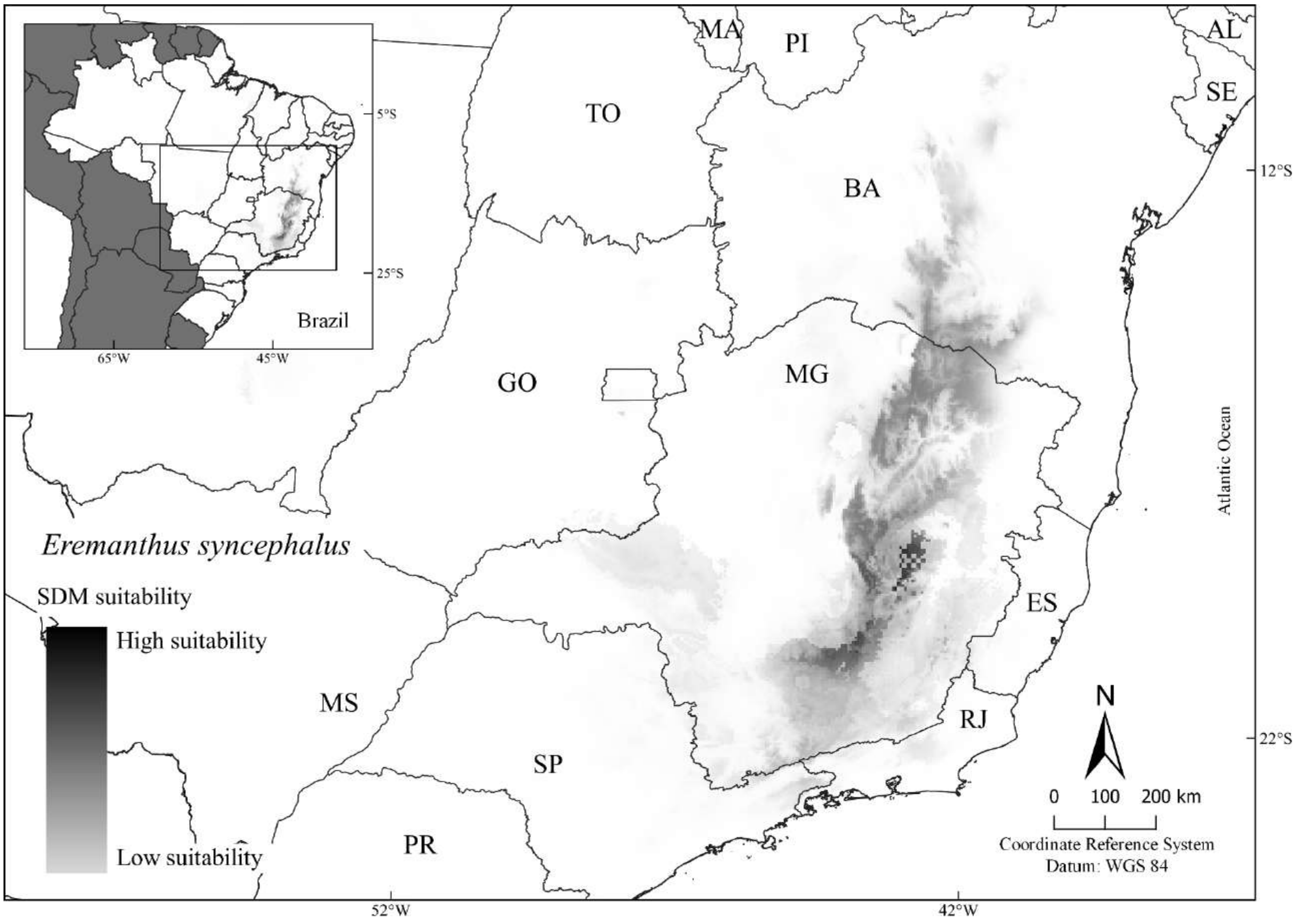

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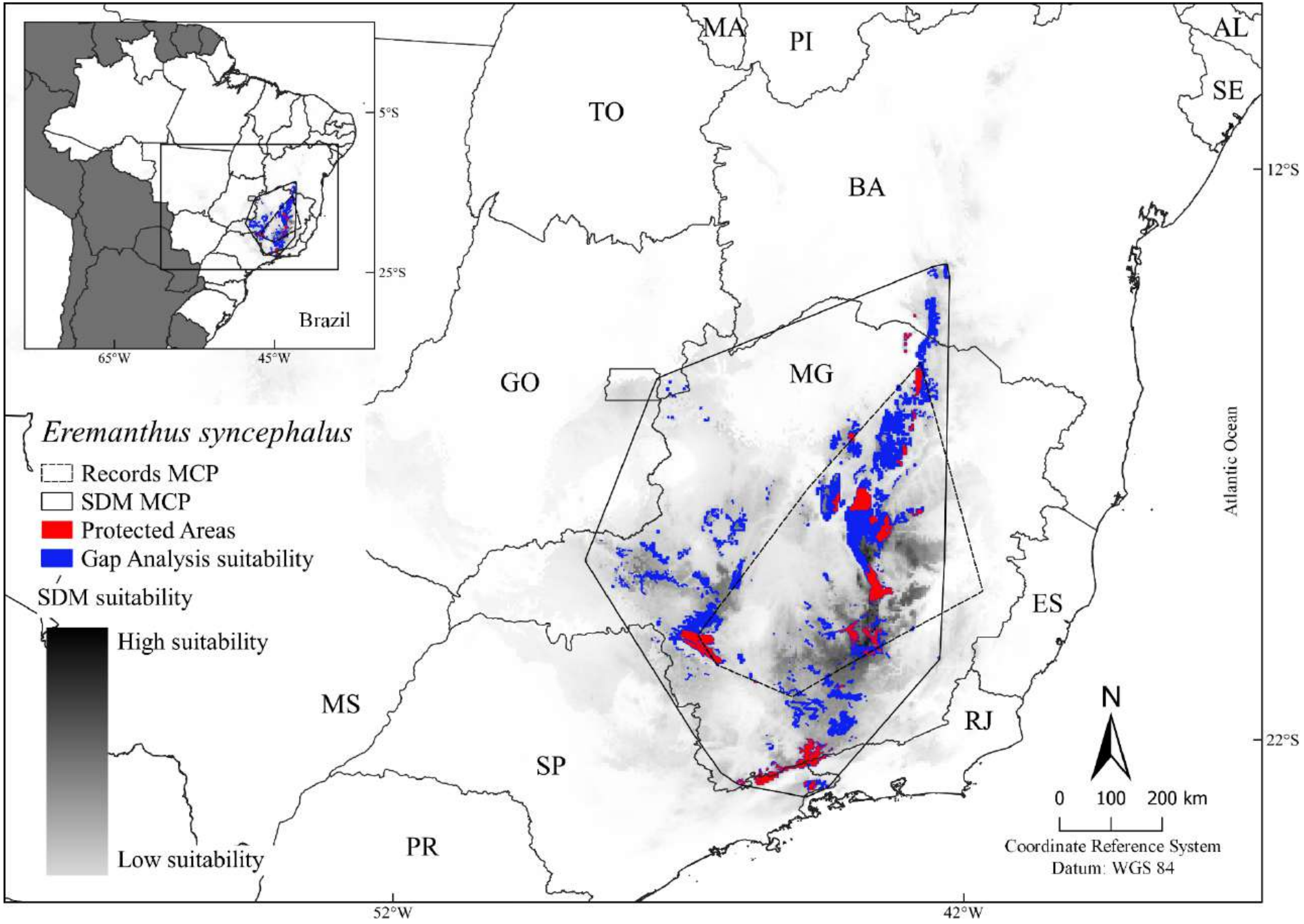

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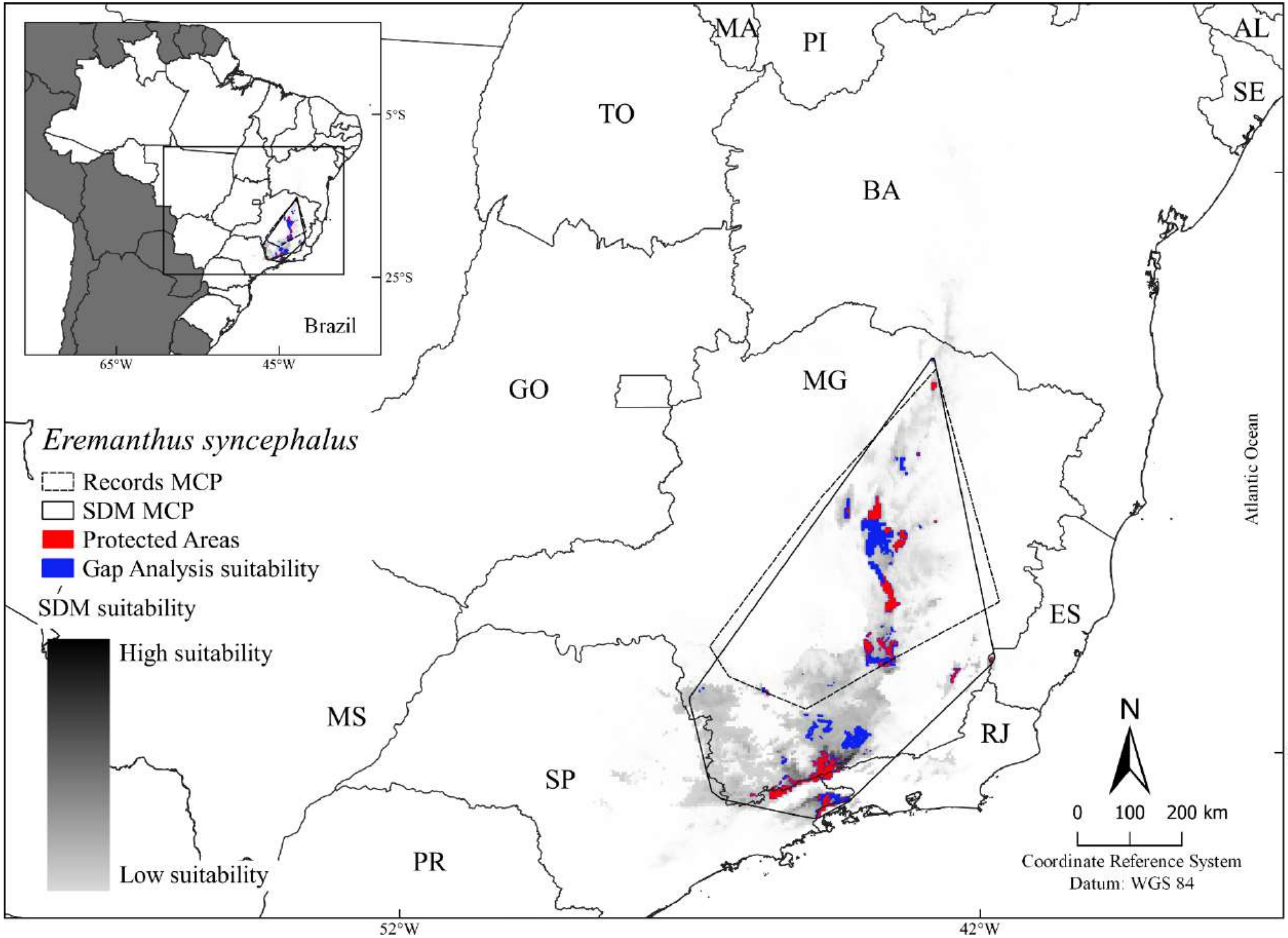

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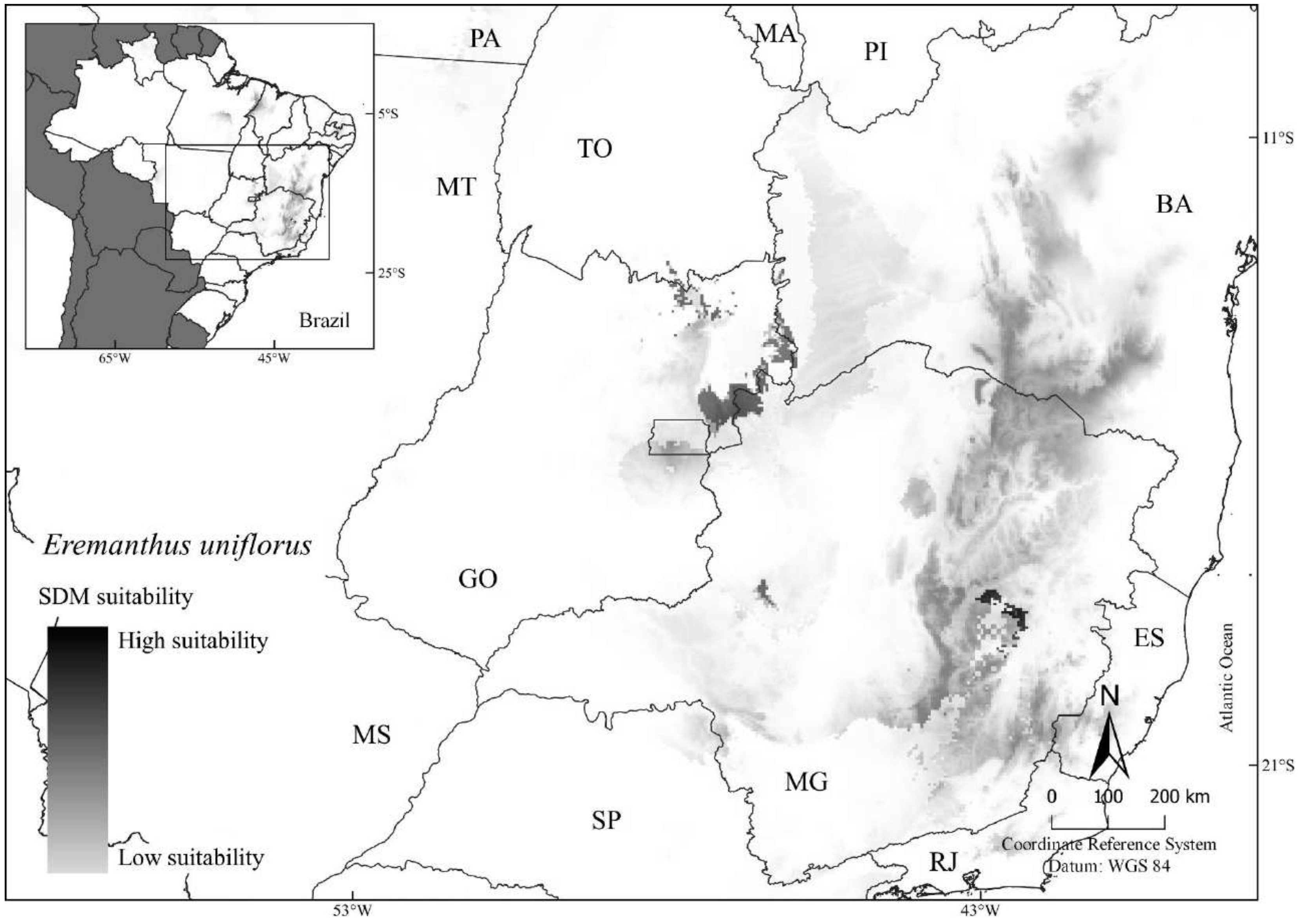

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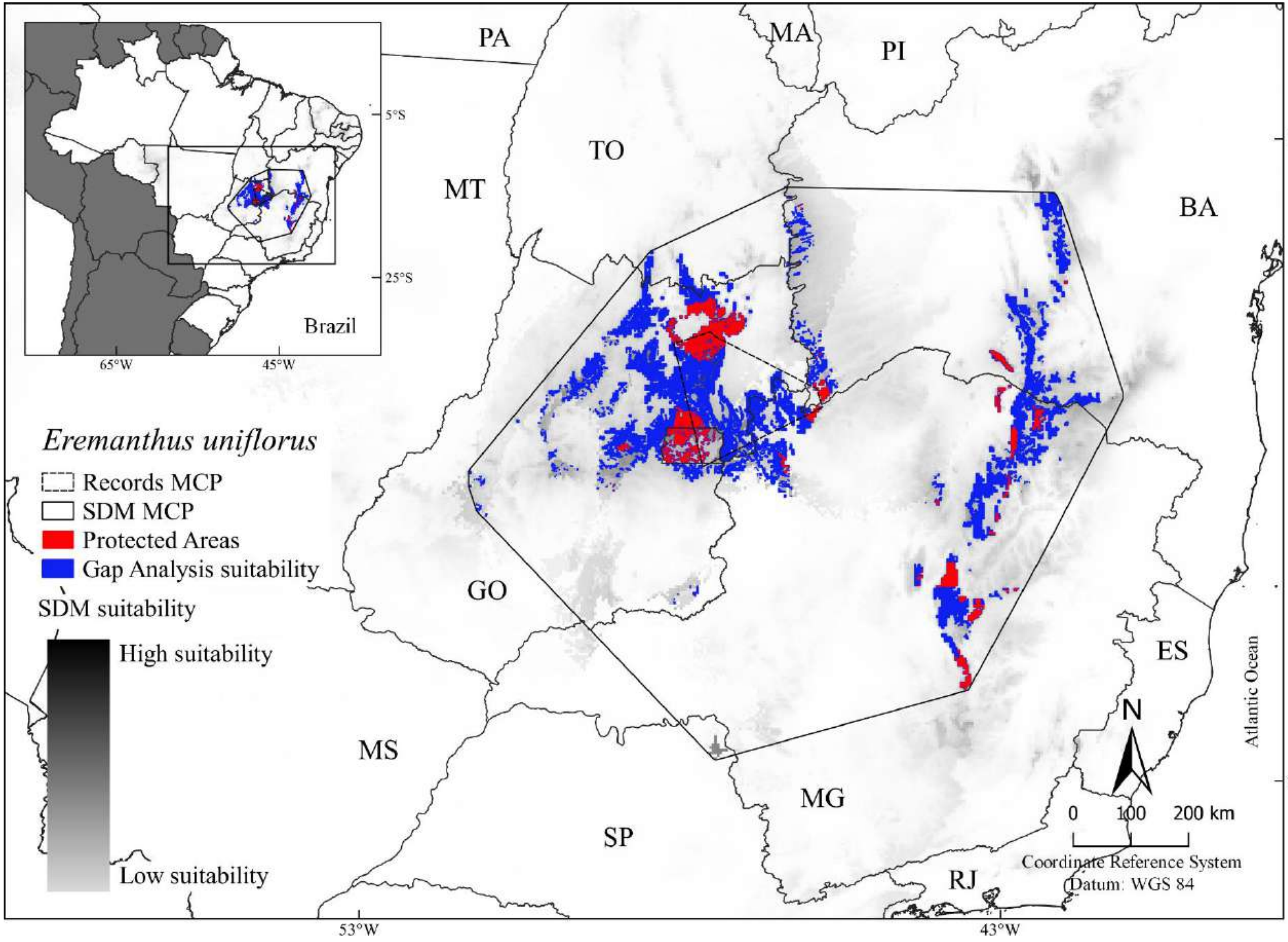

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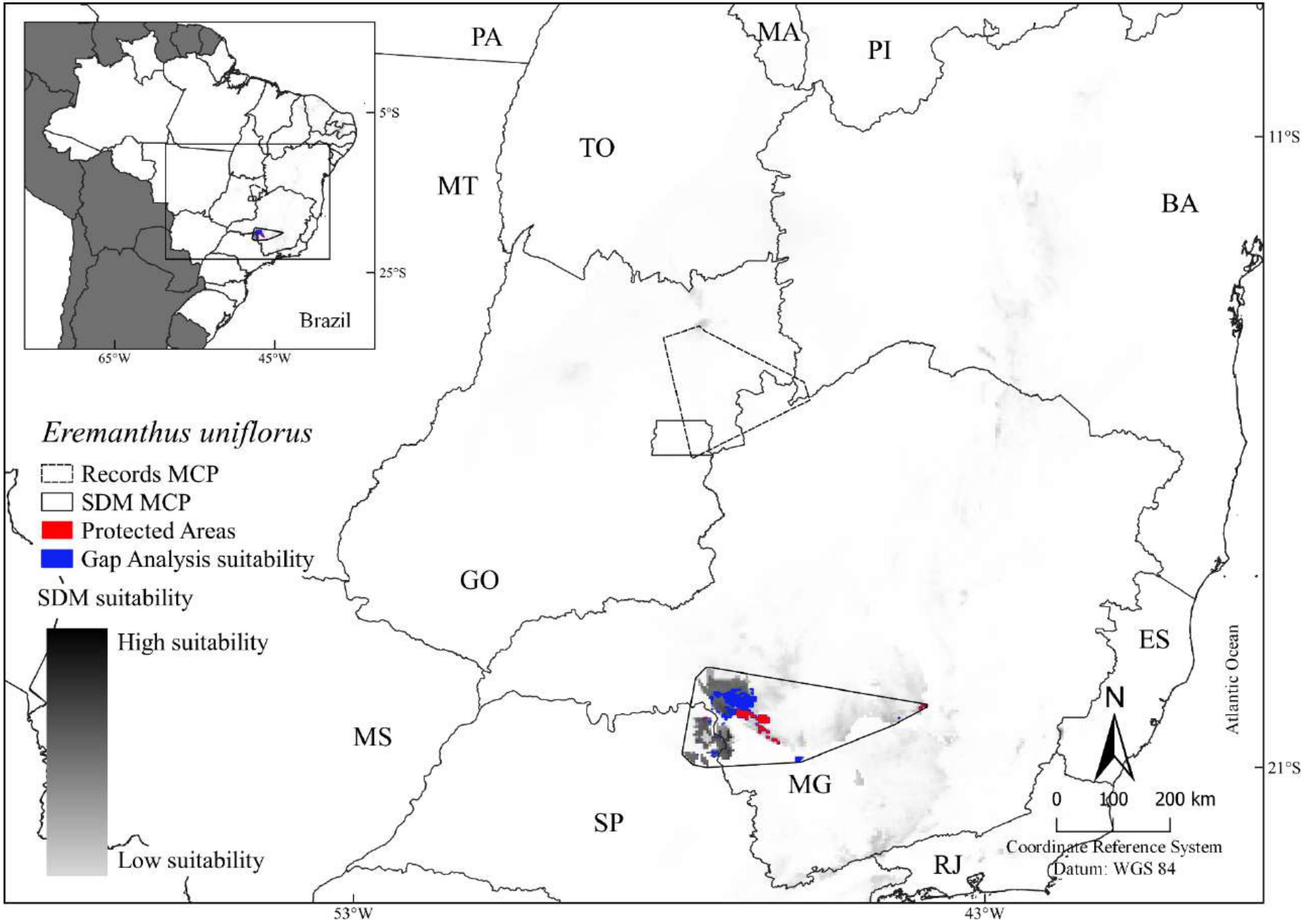

5 CONSIDERAÇÕES FINAIS

Os resultados obtidos através das análises realizadas corroboraram com estudos de outros autores e trouxeram esclarecimentos importantes para o grupo. Foi demonstrado maior resolução das linhagens na árvore filogenética de Lychnophorinae, além de formalizar o monofiletismo de grande parte dos gêneros e estimar o surgimento do grupo no Mioceno. As características morfológicas avaliadas tiveram um importante impacto na composição atual do grupo, evidenciando a importância adaptativa em um período de maior diversificação das linhagens. Isso demonstra que apesar das condições climáticas oscilantes do Pleistoceno as linhagens da subtribo se mostraram bastante resilientes e encontraram meios de permanecer na história evolutiva.

Os estudos biogeográficos confirmaram a grande importância do Espinhaço Meridional para a história macroevolutiva do grupo, não apenas por reconhecer como área de origem da subtribo, mas também por mostrar que o evento de dispersão por efeito fundador foi o principal processo biogeográfico que influenciou a distribuição das espécies. É bastante provável que os eventos climáticos juntamente com o surgimento de estados de caracteres chave durante o Pleistoceno impulsionaram as espécies a colonizar novas áreas nas linhagens mais recentes, porém, é possível constatar também que as áreas de campos rupestres funcionaram como um importante refúgio para algumas linhagens, apresentando, inclusive, uma manutenção de nichos ancestrais. Outro fator importante foi a evidência de compartilhamento de espécies com o cerrado, evidenciado por evento de dispersão de origem deste ambiente para a Cadeia do Espinhaço.

Apesar da modelagem de nicho e avaliação de risco de extinção terem sido realizados em um gênero específico de Lychnophorinae, é possível extrapolar as inferências para a subtribo como um todo, já que *Eremanthus* é um gênero bastante representativo. De todo modo, os estudos realizados serviram para enfatizar a importância da aplicação e integração dos métodos como forma de esclarecer melhor os possíveis fatores que determinam as áreas de adequabilidade ambiental e limitam as distribuições das espécies. É possível prever que em cenários futuros a extinção de certas espécies possui grande probabilidade de ocorrer, já que os eventos que pressionam as espécies a este destino ocorrem de forma célere e pouco controlada. É evidente que diversos outros fatores podem de fato mudar o curso das espécies, inclusive de forma pouco previsível, entretanto, os resultados revelam que o clima sempre foi um importante fator inserido na história de Lychnophorinae e que certamente influenciou e continuará influenciando o trajeto evolutivo desse importante grupo botânico.

REFERÊNCIAS

ABOUHEIF, E. A method for testing the assumption of phylogenetic independence in comparative data. **Evolutionary Ecology Research**, v. 1, p. 895–909, 1999.

ABRAHÃO, A. et al. Soil types select for plants with matching nutrient-acquisition and -use traits in hyperdiverse and severely nutrient-impoverished campos rupestres and cerrado in Central Brazil. **Journal of Ecology**, v. 107, n. 3, p. 1302–1316, 1 maio 2019.

AB’SÁBER, A. N. The natural organization of Brazilian inter-and subtropical landscapes. **Revista do Instituto Geológico**, v. 21, n. 1–2, p. 57–70, 2000.

AGUIAR, A. J. C. et al. Biogeography and early diversification of Tapinotaspidini oil-bees support presence of Paleocene savannas in South America. **Molecular Phylogenetics and Evolution**, v. 143, 1 fev. 2020.

ALCANTARA, S.; REE, R. H.; MELLO-SILVA, R. Accelerated diversification and functional trait evolution in Velloziaceae reveal new insights into the origins of the campos rupestres’ exceptional floristic richness. **Annals of Botany**, v. 122, n. 1, p. 165–180, 2018.

ALVARES, C. A. et al. Köppen’s climate classification map for Brazil. **Meteorologische Zeitschrift**, v. 22, n. 6, p. 711–728, 2013.

ALVES, F. V. S.; LOEUILLE, B. F. P. Geographic distribution patterns of species of the subtribe Lychnophorinae (Asteraceae: Vernonieae). **Rodriguésia**, v. 72, 2021.

ALVES, R. J. V. et al. Circumscribing campo rupestre – megadiverse Brazilian rocky montane savanas. **Brazilian Journal of Biology**, v. 74, n. 2, p. 355–362, 2014.

ALVES, R. J. V. et al. Brazilian legislation on genetic heritage harms Biodiversity Convention goals and threatens basic biology research and education. **Anais da Academia Brasileira de Ciências**, v. 90, n. 2, p. 1279–1284, abr. 2018.

ALVES, R. J. V.; KOLBEK, J. Can campo rupestre vegetation be floristically delimited based on vascular plant genera? **Plant Ecology**, v. 207, n. 1, p. 67–79, 25 mar. 2010.

AMARAL, A. G. et al. Richness pattern and phytogeography of the Cerrado herb–shrub flora and implications for conservation. **Journal of Vegetation Science**, v. 28, n. 4, p. 848–858, 1 jul. 2017.

BACHELET, C. Pré-História no Cerrado: Análises antracologicas dos abrigos de Santa Elina e da Cidade de Pedra (Mato Grosso). **Fronteiras: Journal of Social, Technological and Environmental Science**, v. 3, n. 2, p. 96, 28 dez. 2014.

BAELE, G. et al. Improving the Accuracy of Demographic and Molecular Clock Model Comparison While Accommodating Phylogenetic Uncertainty. **Molecular Biology and Evolution**, v. 29, n. 9, p. 2157–2167, set. 2012.

BALLESTEROS-MEJIA, L.; LIMA, J. S.; COLLEVATTI, R. G. Spatially-explicit analyses reveal the distribution of genetic diversity and plant conservation status in Cerrado biome. **Biodiversity and Conservation**, v. 29, n. 5, p. 1537–1554, 29 abr. 2020.

BARBOSA, A. S. **Sistema Biogeográfico Do Cerrado: Alguns Elementos Para Sua Caracterização**. Goiânia: Editora UCG, 1996.

BARBOSA, N. P. DE U.; FERNANDES, G. W.; SANCHEZ-AZOFEIFA, A. A relict species restricted to a quartzitic mountain in tropical America: an example of microrefugium? **Acta Botanica Brasilica**, v. 29, n. 3, p. 299–309, set. 2015.

BARBOSA, N. P. U. **Modelagem de Distribuição Aplicada aos Campos Rupestres**. (Doctoral dissertation, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil): [s.n.].

BARRES, L. et al. Pleistocene climatic changes drove dispersal and isolation of Richterago discoidea (Asteraceae), an endemic plant of campos rupestres in the central and eastern Brazilian sky islands. **Biological Journal of the Linnean Society**, v. 189, p. 132–152, 2019.

BATISTA, E. K. L. et al. An evaluation of contemporary savanna fire regimes in the Canastra National Park, Brazil: Outcomes of fire suppression policies. **Journal of Environmental Management**, v. 205, p. 40–49, jan. 2018.

BENITES, V. DE M. et al. Soils associated with rock outcrops in the Brazilian mountain ranges Mantiqueira and Espinhaço. **Revista Brasileira de Botânica**, v. 30, n. 4, p. 569–577, dez. 2007.

BENITES, V. DE M. et al. Solos e Vegetação Nos Complexos Rupestres de Altitude da Mantiqueira e do Espinhaço. **Floresta e Ambiente**, v. 10, n. 1, p. 76–85, 29 jun. 2003.

BENTHAM, G.; HOOKER, J. D. Compositae. In: BENTHAM, G.; HOOKER, J. D. (Eds.). **Genera plantarum**. London: Reeve & Co., London and Williams and Norgate, 1873. v. 2, Part 1p. 163–533.

BEUCHLE, R. et al. Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. **Applied Geography**, v. 58, p. 116–127, mar. 2015.

BITENCOURT, C. et al. The worrying future of the endemic flora of a tropical mountain range under climate change. **Flora - Morphology, Distribution, Functional Ecology of Plants**, v. 218, p. 1–10, fev. 2016.

BITENCOURT, C.; RAPINI, A. Centres of endemism in the espinhaço range: Identifying cradles and museums of asclepiadoideae (apocynaceae). **Systematics and Biodiversity**, v. 11, n. 4, p. 525–536, 1 dez. 2013.

BLOMBERG, S. P.; GARLAND, T.; IVES, A. R. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. **Evolution**, v. 57, n. 4, p. 717–745, abr. 2003.

BOANARES, D. et al. Foliar water-uptake strategies are related to leaf water status and gas exchange in plants from a ferruginous rupestrian field. **American Journal of Botany**, v. 106, n. 7, p. 935–942, 7 jul. 2019.

BONATELLI, I. A. S. et al. Interglacial microrefugia and diversification of a cactus species complex: phylogeography and palaeodistributional reconstructions for Pilosocereus aurisetus and allies. **Molecular Ecology**, v. 23, n. 12, p. 3044–3063, jun. 2014.

BONFIM E CÂNDIDO, J.; LOEUILLE, B. Two New Species of Lychnophorella (Vernonieae, Asteraceae) from the Chapada Diamantina, Bahia State, Brazil. **Systematic Botany**, v. 45, n. 2, p. 379–386, 13 maio 2020.

BREMER, K.; WANNTORP, H. PHYLOGENETIC SYSTEMATICS IN BOTANY. **TAXON**, v. 27, n. 4, p. 317–329, 27 ago. 1978.

BROWN, J. W.; SMITH, S. A. The Past Sure is Tense: On Interpreting Phylogenetic Divergence Time Estimates. **Systematic Biology**, v. 67, n. 2, p. 340–353, 1 mar. 2018.

CAMPOS, L. et al. Biogeographical Review of Asteraceae in the Espinhaço Mountain Range, Brazil. **Botanical Review**, v. 85, n. 4, p. 293–336, 1 dez. 2019.

BRUM, M. et al. Coordination of rooting depth and leaf hydraulic traits defines drought-related strategies in the campos rupestres, a tropical montane biodiversity hotspot. **Plant and Soil**, v. 420, n. 1–2, p. 467–480, 20 nov. 2017.

CÂNDIDO, J. B. E; LOEUILLE, B. Three new species of Piptolepis (Vernonieae, Asteraceae) from the Diamantina Plateau, Minas Gerais, Brazil. **Systematic Botany**, v. 46, n. 2, p. 493–503, 11 ago. 2021.

CARMO, F. F. DO; JACOBI, C. M. A vegetação de canga no Quadrilátero Ferrífero, Minas Gerais: caracterização e contexto fitogeográfico. **Rodriguésia**, v. 64, n. 3, p. 527–541, set. 2013.

CHAVES, D. A. et al. Diamonds and Daisies: Floristics and Conservation of Asteraceae in One of Brazil's Major Centers of Endemism. **Tropical Conservation Science**, v. 12, p. 1–18, 2019a.

CHAVES, D. A. et al. Geographic space, relief, and soils predict plant community patterns of Asteraceae in rupestrian grasslands, Brazil. **Biotropica**, v. 51, n. 2, p. 155–164, mar. 2019b.

CHEMALE, F. et al. Unravelling a Proterozoic basin history through detrital zircon geochronology: The case of the Espinhaço Supergroup, Minas Gerais, Brazil. **Gondwana Research**, v. 22, n. 1, p. 200–206, jul. 2012.

COLLEVATTI, R. G. et al. Phylogeography of Tibouchina papyrus (Pohl) Toledo (Melastomataceae), an endangered tree species from rocky savannas, suggests bidirectional expansion due to climate cooling in the Pleistocene. **Ecology and Evolution**, v. 2, n. 5, p. 1024–1035, maio 2012.

COLLI, G. R.; VIEIRA, C. R.; DIANESE, J. C. Biodiversity and conservation of the Cerrado: recent advances and old challenges. **Biodiversity and Conservation**, v. 29, n. 5, p. 1465–1475, 1 abr. 2020.

COLLI-SILVA, M.; VASCONCELOS, T. N. C.; PIRANI, J. R. Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. **Journal of Biogeography**, v. 46, n. 8, p. 1723–1733, 8 ago. 2019.

CONCEIÇÃO, A. A. et al. Rupestrian grassland vegetation, diversity, and origin. In: FERNANDES, G. W. (Ed.). **Ecology and Conservation of Mountaintop Grasslands in Brazil**. Cham: Springer International Publishing, 2016. p. 105–128.

CORDEIRO, G. G. et al. Factors affecting the effectiveness of riparian buffers in retaining sediment: an isotopic approach. **Environmental Monitoring and Assessment**, v. 192, n. 11, 1 nov. 2020.

CRUZ, A. J. DO R. et al. Lizard fauna (Squamata, Sauria) from Serra do Ouro Branco, southern Espinhaço Range, Minas Gerais, Brazil. **Check List**, v. 10, n. 6, p. 1290–1299, 2014.

DANDERFER, A. et al. New geochronological constraints on the geological evolution of Espinhaço basin within the São Francisco Craton-Brazil. **Precambrian Research**, v. 170, n. 1–2, p. 116–128, abr. 2009.

DANDERFER, A.; DARDENNE, M. A. TECTONOESTRATIGRAFIA DA BACIA ESPINHAÇO NA PORÇÃO CEN-TRO-NORTE DO CRÁTON DO SÃO FRANCISCO: REGISTRO DE UMA EVOLUÇÃO POLIISTÓRICA DESCONTÍNUA. **Revista Brasileira de Geociências**, v. 32, n. 4, p. 449–460, 2002.

DANTAS, V. DE L.; BATALHA, M. A. Vegetation structure: Fine scale relationships with soil in a cerrado site. **Flora: Morphology, Distribution, Functional Ecology of Plants**, v. 206, n. 4, p. 341–346, abr. 2011.

DANTAS, V. L.; PAUSAS, J. G. Megafauna biogeography explains plant functional trait variability in the tropics. **Global Ecology and Biogeography**, v. 29, n. 8, p. 1288–1298, 1 ago. 2020.

DAYRELL, R. L. C. et al. Ontogenetic shifts in plant ecological strategies. **Functional Ecology**, v. 32, n. 12, p. 2730–2741, 1 dez. 2018.

DURIGAN, G.; RATTER, J. A. The need for a consistent fire policy for Cerrado conservation. **Journal of Applied Ecology**, v. 53, n. 1, p. 11–15, 1 fev. 2016.

DUSSIN, I. A.; DUSSIN, T. M. SUPERGRUPO ESPINHAÇO: MODELO DE EVOLUÇÃO GEODINÂMICA. **Geonomos**, 1 jul. 1995.

DUTRA E SILVA, S. Challenging the environmental history of the Cerrado: Science, biodiversity and politics on the Brazilian agricultural frontier. **Historia Ambiental Latinoamericana y Caribena**, v. 10, n. 1, p. 82–116, 7 maio 2020.

ECHTERNACHT, L. et al. Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil. **Flora: Morphology, Distribution, Functional Ecology of Plants**, v. 206, n. 9, p. 782–791, set. 2011.

ELLER, C. B.; LIMA, A. L.; OLIVEIRA, R. S. Cloud forest trees with higher foliar water uptake capacity and anisohydric behavior are more vulnerable to drought and climate change. **New Phytologist**, v. 211, n. 2, p. 489–501, jul. 2016.

ENDRESS, P. K.; DOYLE, J. A. Reconstructing the ancestral angiosperm flower and its initial specializations. **American Journal of Botany**, v. 96, n. 1, p. 22–66, jan. 2009.

ESPÍRITO-SANTO, M. M. et al. Understanding patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 371, n. 1703, p. 20150435, 19 set. 2016.

FARINA, F. et al. The Archean–Paleoproterozoic evolution of the Quadrilátero Ferrífero (Brasil): Current models and open questions. **Journal of South American Earth Sciences**, v. 68, p. 4–21, 2016.

FERNANDES, G. W. et al. **Cerrado: em busca de soluções sustentáveis**. Rio de Janeiro: Vertentes Produções Artísticas, 2016.

FERNANDES, G. W. et al. Dismantling Brazil’s science threatens global biodiversity heritage. **Perspectives in Ecology and Conservation**, v. 15, n. 3, p. 239–243, jul. 2017.

FERNANDES, G. W. et al. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. **Biodiversity and Conservation**, v. 27, n. 10, p. 2587–2603, 1 ago. 2018.

FERNANDES, G. W. et al. Biodiversity and ecosystem services in the Campo Rupestre: A road map for the sustainability of the hottest Brazilian biodiversity hotspot. **Perspectives in Ecology and Conservation**, 1 out. 2020.

FERREIRA, R. Q. DE S. et al. Diversidade florística do estrato arbustivo arbóreo de três áreas de cerrado sensu stricto, Tocantins. **Desafios - Revista Interdisciplinar da Universidade Federal do Tocantins**, v. 4, n. 2, p. 69–82, 2017.

FERRER, M. M.; GOOD-AVILA, S. V. Macrophylogenetic analyses of the gain and loss of self-incompatibility in the Asteraceae. **New Phytologist**, v. 173, n. 2, p. 401–414, jan. 2007.

FLORA DO BRASIL 2020: BRAZIL FLORA GROUP. Version 393.335. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. Checklist dataset https://doi.org/10.15468/1mtkaw, 2022.

FOREST, F. Calibrating the Tree of Life: fossils, molecules and evolutionary timescales. **Annals of Botany**, v. 104, n. 5, p. 789–794, out. 2009.

FRANÇOSO, R. D. et al. Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. **Natureza e Conservacao**, v. 13, n. 1, p. 35–40, 2015.

FRANS, V. F. et al. Integrated SDM database: Enhancing the relevance and utility of species distribution models in conservation management. **Methods in Ecology and Evolution**, 7 nov. 2021.

FRITZ, S. A.; PURVIS, A. Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. **Conservation Biology**, v. 24, n. 4, p. 1042–1051, ago. 2010.

GAGEN, E. J. et al. Biogeochemical processes in canga ecosystems: Armoring of iron ore against erosion and importance in iron duricrust restoration in Brazil. **Ore Geology Reviews**, v. 107, p. 573–586, 1 abr. 2019.

GITTLEMAN, J. L.; KOT, M. Adaptation: Statistics and a Null Model for Estimating Phylogenetic Effects. **Systematic Zoology**, v. 39, n. 3, p. 227, set. 1990.

GIULIETTI, A. M.; PIRANI, J. R. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia, Brazil. In Vanzolini, P.E. and Heyer, W.R. (eds), Proceedings of a workshop on neotropical distribution patterns. **Academia Brasileira de Ciencias**, p. 39–69, 1988.

GIULIETTI, A. M.; PIRANI, J. R.; HARLEY, R. M. Espinhaço range region Eastern Brazil. In: S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, & A. C. Hamilton (Eds), Centres of plant diversity. A guide and strategies for the conservation, Vol. 3. The Americas. **WWF/IUCN**, p. 397–404, 1997.

GOMES, F. M. B.; LOEUILLE, B. Three New Species of Lychnocephalus (Asteraceae: Vernonieae) from the Serra do Cipó, Minas Gerais, Brazil. **Systematic Botany**, v. 46, n. 2, p. 476–485, 11 ago. 2021.

GOMES, L.; MIRANDA, H. S.; BUSTAMANTE, M. M. DA C. How can we advance the knowledge on the behavior and effects of fire in the Cerrado biome? **Forest Ecology and Management**, v. 417, p. 281–290, 15 maio 2018.

GRECCHI, R. C. et al. Land use and land cover changes in the Brazilian Cerrado: A multidisciplinary approach to assess the impacts of agricultural expansion. **Applied Geography**, v. 55, p. 300–312, dez. 2014.

GUINDON, S. From Trajectories to Averages: An Improved Description of the Heterogeneity of Substitution Rates Along Lineages. **Systematic Biology**, v. 62, n. 1, p. 22–34, 1 jan. 2013.

GUISAN, A. et al. Predicting species distributions for conservation decisions. **Ecology Letters**, v. 16, n. 12, p. 1424–1435, dez. 2013.

HUNKE, P. et al. The Brazilian Cerrado: Assessment of water and soil degradation in catchments under intensive agricultural use. **Ecohydrology**, v. 8, n. 6, p. 1154–1180, 1 set. 2015.

INGLIS, P. W.; CAVALCANTI, T. B. A molecular phylogeny of the genus diplusodon (Lythraceae), endemic to the campos rupestres and cerrados of South America. **Taxon**, v. 67, n. 1, p. 66–82, 1 mar. 2018.

JACOBI, C. M.; CARMOS, F. F. DO. Diversidade dos campos rupestres ferruginosos no Quadrilátero Ferrífero, MG. **Megadiversidade**, v. 4, n. 1–2, p. 25–33, 2008.

KARIYAWASAM, C. S.; KUMAR, L.; RATNAYAKE, S. S. Invasive Plants Distribution Modeling: A Tool for Tropical Biodiversity Conservation With Special Reference to Sri Lanka. **Tropical Conservation Science**, v. 12, 1 jul. 2019.

KEELEY, S. C.; CANTLEY, J. T.; GALLAHER, T. J. The “evil tribe” spreads across the land: A dated molecular phylogeny provides insight into dispersal, expansion, and biogeographic relationships within one of the largest tribes of the sunflower family (Vernonieae: Compositae). **American Journal of Botany**, v. 108, n. 3, p. 505–519, 1 mar. 2021.

KEELEY, S. C.; FORSMAN, Z. H.; CHAN, R. A phylogeny of the “evil tribe” (Vernonieae: Compositae) reveals Old/New World long distance dispersal: Support from separate and combined congruent datasets (trnL-F, ndhF, ITS). **Molecular Phylogenetics and Evolution**, v. 44, n. 1, p. 89–103, jul. 2007.

KIM, J. S.; KIM, J.-H. Updated molecular phylogenetic analysis, dating and biogeographical history of the lily family (Liliaceae: Liliales). **Botanical Journal of the Linnean Society**, v. 187, n. 4, p. 579–593, 27 jul. 2018.

KLINK, C. A. et al. The Role of Vegetation on the Dynamics of Water and Fire in the Cerrado Ecosystems: Implications for Management and Conservation. **Plants**, v. 9, n. 12, p. 1803, 18 dez. 2020.

KLINK, C.; MACHADO, R. B. A conservação do Cerrado brasileiro. **Megadiversidade**, v. 1, n. 1, p. 149–155, 2005.

KUCHENBECKER, M.; SANGLARD, J. C. D. The role of detachment and interlayer shear zones in the structural evolution of the southern Espinhaço range, eastern Brazil. **Journal of South American Earth Sciences**, v. 84, p. 343–350, 1 jul. 2018.

LE STRADIC, S. et al. Regeneration after fire in campo rupestre: Short- and long-term vegetation dynamics. **Flora: Morphology, Distribution, Functional Ecology of Plants**, v. 238, p. 191–200, 1 jan. 2018.

LEE, M. S. Y.; OLIVER, P. M.; HUTCHINSON, M. N. Phylogenetic uncertainty and molecular clock calibrations: A case study of legless lizards (Pygopodidae, Gekkota). **Molecular Phylogenetics and Evolution**, v. 50, n. 3, p. 661–666, mar. 2009.

LENZA, E.; KLINK, C. A. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. **Revista Brasileira de Botânica**, v. 29, n. 4, p. 627–638, dez. 2006.

LIMA, J. E. F. W. et al. **The Relevance Of The Cerrado’s Water Resources To The Brazilian Development**. IWRA World Water Congress 2011. **Anais**...2011.

LITSIOS, G.; SALAMIN, N. Effects of Phylogenetic Signal on Ancestral State Reconstruction. **Systematic Biology**, v. 61, n. 3, p. 533–538, 1 maio 2012.

LOEUILLE, B. et al. A phylogenetic analysis of Lychnophorinae (asteraceae: Vernonieae) based on molecular and morphological data. **Systematic Botany**, v. 40, n. 1, p. 299–315, 2015.

LOEUILLE, B.; KEELEY, S. C.; PIRANI, J. R. Systematics and evolution of syncephaly in American Vernonieae (Asteraceae) with emphasis on the Brazilian subtribe Lychnophorinae. **Systematic Botany**, v. 40, n. 1, p. 286–298, 2015.

LOEUILLE, B.; SEMIR, J.; PIRANI, J. R. A synopsis of Lychnophorinae (Asteraceae: Vernonieae). **Phytotaxa**, v. 398, n. 1, p. 1–139, 22 mar. 2019.

LOEUILLE, B. et al. Three new species of Lychnophorinae from the Brazilian Central Plateau (Asteraceae: Vernonieae). **Phytotaxa**, v. 531, n. 3, p. 249–266, 21 jan. 2022.

LOSOS, J. B. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. **Ecology Letters**, v. 11, n. 10, p. 995–1003, out. 2008.

LUSA, M. G.; LOEUILLE, B. F. P.; APPEZZATO-DA-GLÓRIA, B. First record of phytomelanin in aerial vegetative organs and its evolutionary implications in Lychnophorinae (Vernonieae: Asteraceae). **Perspectives in Plant Ecology, Evolution and Systematics**, v. 33, p. 18–33, ago. 2018.

MAGALHÃES, G. M. Sobre os cerrados de Minas Gerais. **Anais da Academia Brasileira de Ciências**, v. 38, n. ssupl, p. 59–70, 1966.

MALIK, S. et al. Phylogeny and biogeography of Artemisia subgenus seriphidium (Asteraceae: Anthemideae). **Taxon**, v. 66, n. 4, p. 934–952, 2017.

MANDEL, J. R. et al. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. **Proceedings of the National Academy of Sciences**, v. 116, n. 28, p. 14083–14088, 2019.

MARQUES, D. et al. Flowers to Òsanyìn: Lychnophora osanyiniana (Asteraceae: Vernonieae) a new “arnica da serra” from Minas Gerais, Brazil. **Phytotaxa**, v. 491, n. 1, p. 57–64, 17 mar. 2021.

MATTOS, J. S. DE et al. Plant phylogenetic diversity of tropical mountaintop rocky grasslands: local and regional constraints. **Plant Ecology**, v. 220, n. 12, p. 1119–1129, 6 dez. 2019.

MAXTED, N. et al. Gap analysis: a tool for complementary genetic conservation assessment. **Diversity and Distributions**, v. 14, n. 6, p. 1018–1030, nov. 2008.

MIRANDA, A. C. et al. Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. **Plant, Cell and Environment**, v. 20, n. 3, p. 315–328, 1997.

MITRE, S. K. et al. Nutrient and water dynamics of Amazonian canga vegetation differ among physiognomies and from those of other neotropical ecosystems. **Plant Ecology**, v. 219, n. 11, p. 1341–1353, 1 nov. 2018.

MONTEIRO, B. L. et al. Pollination in the *campo rupestre*: a test of hypothesis for an ancient tropical mountain vegetation. **Biological Journal of the Linnean Society**, v. 133, n. 2, p. 512–530, 1 jun. 2021.

MONTEIRO, H. S.; VASCONCELOS, P. M. P.; FARLEY, K. A. A Combined (U-Th)/He and Cosmogenic 3He Record of Landscape Armoring by Biogeochemical Iron Cycling. **Journal of Geophysical Research: Earth Surface**, v. 123, n. 2, p. 298–323, 1 fev. 2018.

MONTEIRO, L. et al. Conservation priorities for the threatened flora of mountaintop grasslands in Brazil. **Flora**, v. 238, p. 234–243, jan. 2018.

MORANDI, P. S. et al. Tree diversity and above-ground biomass in the South America Cerrado biome and their conservation implications. **Biodiversity and Conservation**, v. 29, n. 5, p. 1519–1536, 28 abr. 2020.

MOTA, G. S. et al. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. **Flora: Morphology, Distribution, Functional Ecology of Plants**, v. 238, p. 32–42, 1 jan. 2018.

MOTA, N. F. DE O. et al. Cangas da Amazônia: a vegetação única de Carajás evidenciada pela lista de fanerógamas. **Rodriguésia**, v. 69, n. 3, p. 1435–1488, 1 set. 2018.

MOURÃO, A.; STEHMANN, J. R. Levantamento da flora do campo rupestre sobre canga hematítica couraçada remanescente na Mina do Brucutu, Barão de Cocais, Minas Gerais, Brasil. **Rodriguésia**, v. 58, n. 4, p. 775–786, out. 2007.

MÜGGE, F. L. et al. Native plant species with economic value from Minas Gerais and Goiás: a discussion on the currentness of the data recovered by the French naturalist Auguste de Saint-Hilaire. **Horticultura Brasileira**, v. 34, n. 4, p. 455–462, dez. 2016.

MÜNKEMÜLLER, T. et al. How to measure and test phylogenetic signal. **Methods in Ecology and Evolution**, v. 3, n. 4, p. 743–756, ago. 2012.

NEGREIROS, D. et al. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. **Plant Ecology**, v. 215, n. 4, p. 379–388, 1 abr. 2014.

NEVES, B. B. DE B.; CORDANI, U. G. Tectonic evolution of South America during the Late Proterozoic. **Precambrian Research**, v. 53, n. 1–2, p. 23–40, out. 1991.

NEVES, D. M. et al. Lack of floristic identity in campos rupestres — A hyperdiverse mosaic of rocky montane savannas in South America. **Flora**, v. 238, p. 24–31, 2018.

OLDFIELD, T. E. E. et al. A gap analysis of terrestrial protected areas in England and its implications for conservation policy. **Biological Conservation**, v. 120, n. 3, p. 303–309, dez. 2004.

OLIVEIRA, A. S. et al. Costs and effectiveness of public and private fire management programs in the Brazilian Amazon and Cerrado. **Forest Policy and Economics**, v. 127, 1 jun. 2021.

OLIVEIRA, R. S. et al. Ecophysiology of campos rupestres plants. In: FERNANDES, G. W. (Ed.). **Ecology and Conservation of Mountaintop Grasslands in Brazil**. [s.l.] Springer International Publishing, 2016. p. 227–272.

OMLAND, K. E. The Assumptions and Challenges of Ancestral State Reconstructions. **Systematic Biology**, v. 48, n. 3, p. 604–611, 1999.

OVERBECK, G. E. et al. Global Biodiversity Threatened by Science Budget Cuts in Brazil. **BioScience**, v. 68, n. 1, p. 11–12, 1 jan. 2018.

PACHECO, A. A.; NEVES, A. C. O.; FERNANDES, G. W. Uneven conservation efforts compromise Brazil to meet the Target 11 of Convention on Biological Diversity. **Perspectives in Ecology and Conservation**, v. 16, n. 1, p. 43–48, jan. 2018.

PAGEL, M. Inferring the historical patterns of biological evolution. **Nature**, v. 401, n. 6756, p. 877–884, out. 1999.

PANERO, J. L. et al. Resolution of deep nodes yields an improved backbone phylogeny and a new basal lineage to study early evolution of Asteraceae. **Molecular Phylogenetics and Evolution**, v. 80, p. 43–53, nov. 2014.

PEDROSA-SOARES, A. C.; ALKMIM, F. F. DE. HOW MANY RIFTING EVENTS PRECEDED THE DEVELOPMENT OF THE ARAÇUAÍ-WEST CONGO OROGEN? **Geonomos**, v. 19, n. 2, p. 244–251, 13 fev. 2013.

PENA, J. C. DE C. et al. Impacts of mining activities on the potential geographic distribution of eastern Brazil mountaintop endemic species. **Perspectives in Ecology and Conservation**, v. 15, n. 3, p. 172–178, 1 jul. 2017.

PETERSON, A. T.; ROBINS, C. R. Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation. **Conservation Biology**, v. 17, n. 4, p. 1161–1165, 2003.

PINHEIRO, MHO.; MONTEIRO, R. Contribution to the discussions on the origin of the cerrado biome: Brazilian savanna. **Brazilian Journal of Biology**, v. 70, n. 1, p. 95–102, fev. 2010.

PORTO, M. L.; DA SILVA, M. F. F. Tipos de vegetação metalófila em áreas da serra de Carajás e de Minas Gerais, Brasil. **Acta Botanica Brasilica**, v. 3, n. 2, p. 13–21, 1989.

PRANCE, G. T. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. **Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences**, v. 345, n. 1311, p. 89–99, 29 jul. 1994.

RANGEL, T. F. et al. Phylogenetic uncertainty revisited: Implications for ecological analyses. **Evolution**, v. 69, n. 5, p. 1301–1312, maio 2015.

RATTER, J. A.; RIBEIRO, J. F.; BRIDGEWATER, S. The Brazilian Cerrado Vegetation and Threats to its Biodiversity. **Annals of Botany**, v. 80, n. 3, p. 223–230, set. 1997.

REVELL, L. J.; HARMON, L. J.; COLLAR, D. C. Phylogenetic Signal, Evolutionary Process, and Rate. **Systematic Biology**, v. 57, n. 4, p. 591–601, 1 ago. 2008.

REYES, E. et al. Testing the impact of morphological rate heterogeneity on ancestral state reconstruction of five floral traits in angiosperms. **Scientific Reports**, v. 8, n. 1, p. 9473, 21 dez. 2018.

RIBAS, R. P. et al. Afforestation in the Rupestrian Grasslands: The Augmenting Pressure of Eucalyptus. In: FERNANDES, G. W. (Ed.). **Ecology and Conservation of Mountaintop grasslands in Brazil**. Cham: Springer International Publishing, 2016. p. 395–414.

RIZZINI, C. T. **Tratado de Fitogeografia do Brasil: Aspectos Ecológicos**. São Paulo: [s.n.].

ROBINSON, H. E. Notes on the Lychnophorine genera Chresta and Eremanthus. **Phytologia.**, v. 45, p. 89–100, 1980.

ROBINSON, H. E. Notes on Lychnophorinae from Minas Gerais, Brazil, a synopsis of Lychnophoriopsis Schultz-Bip., and the new genera Anteremanthus and Minasia (Vernonieae: Asteraceae). **Proceedings of the Biological Society of Washington**, v. 105, p. 640–652, 1992.

ROBINSON, H. E. Generic and subtribal classification of American Vernonieae. **Smithsonian Contributions to Botany**, n. 89, p. 1–116, 1999.

RUTSCHMANN, F. Molecular dating of phylogenetic trees: A brief review of current methods that estimate divergence times. **Diversity and Distributions**, v. 12, n. 1, p. 35–48, jan. 2006.

SAADI, A. A GEOMORFOLOGIA DA SERRA DO ESPINHAÇO EM MINAS GERAIS E DE SUAS MARGENS. **Geonomos**, v. 3, n. 1, p. 41–63, 1 jul. 1995.

SAMPAIO, A. J. DE. **Phytogeographia do Brasil**. São Paulo: Editora Nacional, 1938.

SAMPAIO, G. M. S. et al. Influence of weathering and hydrothermal alteration on the REE and δ56Fe composition of iron formation, Cauê Formation, Iron Quadrangle, Brazil. **Chemical Geology**, v. 497, p. 27–40, 10 out. 2018.

SANO, E. E. et al. Land cover mapping of the tropical savanna region in Brazil. **Environmental Monitoring and Assessment**, v. 166, n. 1–4, p. 113–124, 6 jul. 2010.

SANTOS, A. J. B. et al. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in central Brazil. **Functional Ecology**, v. 17, n. 6, p. 711–719, dez. 2003.

SANTOS, J. S. DOS et al. Landscape ecology in the Anthropocene: an overview for integrating agroecosystems and biodiversity conservation. **Perspectives in Ecology and Conservation**, v. 19, n. 1, p. 21–32, jan. 2021.

SCHAEFER, C. E. et al. Solos desenvolvidos sobre Canga Ferruginosa no Brasil: uma revisão crítica e papel ecológico de termiteiros. In: CARMO, F. F. DO; KAMINO, L. H. Y. (Eds.). **Geossistemas Ferruginosos do Brasil**. 1. ed. Belo Horizonte: 3i Editora, 2015. p. 77–102.

SCHMIDT, G. J.; SCHILLING, E. E. Phylogeny and biogeography of Eupatorium (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. **American Journal of Botany**, v. 87, n. 5, p. 716–726, 2000.

SHARAFI, S. M. et al. Integrating environmental gap analysis with spatial conservation prioritization: A case study from Victoria, Australia. **Journal of Environmental Management**, v. 112, p. 240–251, dez. 2012.

SHEN, C.-Z. et al. Clarifying Recent Adaptive Diversification of the Chrysanthemum-Group on the Basis of an Updated Multilocus Phylogeny of Subtribe Artemisiinae (Asteraceae: Anthemideae). **Frontiers in Plant Science**, v. 12, 26 maio 2021.

SILVA, A. C. et al. Solos do topo da Serra São José (Minas Gerais) e suas relações com o paleoclima no Sudeste do Brasil. **Revista Brasileira de Ciência do Solo**, v. 28, n. 3, p. 455–466, jun. 2004.

SILVA, M. F. F. DA; SECCO, R. DE S.; LOBO, M. DA G. A. ASPECTOS ECOLÓGICOS DA VEGETAÇÃO RUPESTRE DA SERRA DOS CARAJÁS, ESTADO DO PARÁ, BRASIL. **Acta Amazonica**, v. 26, n. 1–2, p. 17–44, jun. 1996.

SILVA, T. M. et al. Anatomy and fructan distribution in vegetative organs of Dimerostemma vestitum (Asteraceae) from the campos rupestres. **Anais da Academia Brasileira de Ciências**, v. 87, n. 2, p. 797–812, 9 jun. 2015.

SILVA-MORAES, H. G.; CORDEIRO, I.; FIGUEIREDO, N. FLORA AND FLORISTIC AFFINITIES OF THE CERRADOS OF MARANHÃO STATE, BRAZIL. **Edinburgh Journal of Botany**, v. 76, n. 1, p. 1–21, 24 set. 2018.

SILVEIRA, F. A. O. et al. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. **Plant and Soil**, v. 403, n. 1–2, p. 129–152, 1 jun. 2016.

SIMON, M. F. et al. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. **Proceedings of the National Academy of Sciences**, v. 106, n. 48, p. 20359–20364, 2009.

SIMON, M. F.; PENNINGTON, T. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. **International Journal of Plant Sciences**, v. 173, n. 6, p. 711–723, 2012.

SINISCALCHI, C. M. et al. Phylogenomics Yields New Insight Into Relationships Within Vernonieae (Asteraceae). **Frontiers in Plant Science**, v. 10, 17 out. 2019.

SKIRYCZ, A. et al. Canga biodiversity, a matter of mining. **Frontiers in Plant Science**, v. 5, n. 653, 24 nov. 2014.

SOLTIS, D. E. et al. Evolution of genome size in the angiosperms. **American Journal of Botany**, v. 90, n. 11, p. 1596–1603, nov. 2003.

STEVENS, P. F. Character States, Morphological Variation, and Phylogenetic Analysis: A Review. **Systematic Botany**, v. 16, n. 3, p. 553, jul. 1991.

STRASSBURG, B. B. N. et al. Moment of truth for the Cerrado hotspot. **Nature Ecology and Evolution**, v. 1, n. 4, 23 mar. 2017.

VALERA, C. A. et al. The buffer capacity of riparian vegetation to control water quality in anthropogenic catchments from a legally protected area: A critical view over the Brazilian new forest code. **Water (Switzerland)**, v. 11, n. 3, 2019.

VAN BREUGEL, P. et al. Environmental Gap Analysis to Prioritize Conservation Efforts in Eastern Africa. **PLOS ONE**, v. 10, n. 4, p. e0121444, 9 abr. 2015.

VASCONCELOS, M. F. DE. O que são campos rupestres e campos de altitude nos topos de montanha do leste do Brasil? **Brazilian Journal of Botany**, v. 34, n. 2, p. 241–246, jun. 2011.

VASCONCELOS, P. M.; CARMO, I. DE O. Calibrating denudation chronology through 40Ar/39Ar weathering geochronology. **Earth-Science Reviews**, v. 179, p. 411–435, 1 abr. 2018.

VASCONCELOS, T. N. C. et al. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. **Proceedings of the Royal Society B: Biological Sciences**, v. 287, n. 1923, 25 mar. 2020.

VELAZCO, S. J. E. et al. A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. **Diversity and Distributions**, v. 25, n. 4, p. 660–673, 1 abr. 2019.

VELAZCO, S. J. E. et al. Overprediction of species distribution models in conservation planning: A still neglected issue with strong effects. **Biological Conservation**, v. 252, 1 dez. 2020.

VENTER, O. et al. Targeting Global Protected Area Expansion for Imperiled Biodiversity. **PLoS Biology**, v. 12, n. 6, 2014.

VIANA, P. L. et al. Flora das cangas da Serra dos Carajás, Pará, Brasil: história, área de estudos e metodologia. **Rodriguésia**, v. 67, n. 5spe, p. 1107–1124, 1 dez. 2016.

VIANA, P. L.; LOMBARDI, J. A. Florística e caracterização dos campos rupestres sobre canga na Serra da Calçada, Minas Gerais, Brasil. **Rodriguésia**, v. 58, n. 1, p. 157–177, jan. 2007.

VIEIRA, R. R. S.; PRESSEY, R. L.; LOYOLA, R. The residual nature of protected areas in Brazil. **Biological Conservation**, v. 233, p. 152–161, 1 maio 2019.

WAGSTAFF, S. J.; BREITWIESER, I.; ITO, M. Evolution and biogeography of Pleurophyllum (Astereae, Asteraceae), a small genus of megaherbs endemic to the subantarctic islands. **American Journal of Botany**, v. 98, n. 1, p. 62–75, jan. 2011.

WEN, J. et al. Biogeography: Where do we go from here? **Taxon**, v. 62, n. 5, p. 912–927, 22 out. 2013.

XU, L.-S. et al. Phylogeny, origin and dispersal of Saussurea (Asteraceae) based on chloroplast genome data. **Molecular Phylogenetics and Evolution**, v. 141, p. 106613, dez. 2019.

ZAGO, L. M. S. et al. Biochemical activity in Brazilian Cerrado soils is differentially affected by perennial and annual crops. **Australian Journal of Crop Science**, v. 12, n. 2, p. 235–242, 1 fev. 2018.

ZAPPI, C. et al. Plotting a future for Amazonian canga vegetation in a campo rupestre context. **PLoS ONE**, v. 14, n. 8, 1 ago. 2019.

ANEXO A – LINKS PARA AS NORMAS DE SUBMISSÃO DAS REVISTAS CIENTÍFICAS

INTERNATIONAL JOURNAL OF PLANT SCIENCES (Capítulo 1)

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